Acta Zoologica

INTERNATIONAL JOURNAL FOR ZOOLOGY

founded 1920 by NILS HOLMGREN

EDITOR TORSTEN PEHRSON

Associate Editors BERTIL HANSTRÖM *and* PER ERIC LINDAHL

VOL. 42

1961

OL.
42
961

SVENSKA BOKFÖRLAGET / *Bonniers / Stockholm*
GYLDENDALSKE BOGHANDEL / NORDISK FORLAG / *København*
AKATEEMINEN KIRJAKAUPPA / AKADEMISKA BOKHANDELN / *Helsinki*
WILLIAM HEINEMANN LTD. / *London / Melbourne / Toronto*

SCANDINAVIAN UNIVERSITY BOOKS

Gyldendalske Boghandel — Nordisk Forlag, København

Svenska Bokförlaget — P. A. Norstedt & Söner — Albert Bonnier, Stockholm

Akateeminen Kirjakauppa — Akademiska Bokhandeln, Helsinki

William Heineman Ltd. London / Melbourne / Toronto

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PRINTED IN SWEDEN

STOCKHOLM. ALB. BONNIERS BOKTRYCKERI 1961

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The Development of The Chondrocranium of *Heleophryne Purcelli* Sclater with special Reference to the Palatoquadrate and the Sound-conducting Apparatus

by

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Thesis accepted for the Degree of Doctor of Science at the University of Stellenbosch
Promotor: Prof. C. A. du Toit. Submitted: September, 1959

(Received Febr. 27, 1960)

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The Chondrocranium of Heleophryne Purcelli Sclater

Abstract

A description of the later phases of the ontogeny of the chondrocranium of *Heleophryne purcelli* is given. Special attention has been given to the development of the sound-conducting apparatus and to the structural changes of the palatoquadrate during metamorphosis. The operculum, the pars interna plectri and the pars media plectri are apparently of capsular origin, whereas the pars externa plectri and the anulus tympanicus, which develop from a common blasteme, appear to the be derivatives of the palatoquadrate. It is suggested that the infrapharyngohyal had been incorporated into the otic capsule during the phylogeny, and that it gives rise to the operculum and the pars interna et media plectri, as well as to the floor of the fossa fenestrae ovalis and the otic ledge of the adult. Similarly, the epihyal became incorporated into the posterior portion of the larval palatoquadrate (epimandibular), and gives rise to the pars externa plectri of the adult. The suprapharyngohyal is represented by the otic process and the lateral portion of the parotic crest. The anulus tympanicus is probably the homologue of the stylohyal of fishes. The suprapharyngomandibular and the infrapharyngomandibular are both absent in the adult skull.

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Introduction

In these investigations a study was made of the development of the chondrocranium of *Heleophryne purcelli* from Jonkershoek, Stellenbosch. Special attention was paid to the palatoquadrate and the sound-conducting apparatus of this South African torrent-dwelling anuran. No description is given of the dermal bones connected with the neuro- and viscerocranium; the reader is referred to the work of DU TOIT (1930) who gives an account of the skull of adult *Heleophryne*. RAMASWAMI (1944) describes the chondrocranium of the larva.

In the present paper a more detailed description is given of the later development of the chondrocranium. Unfortunately nothing is known of the breeding habits of this genus, no eggs have ever been found, and the youngest available larvae already have a well-developed chondrocranium. It is therefore left to subsequent workers to give an account of the earlier stages of the development of the chondrocranium.

It is a well-known fact that the sound-conducting apparatus and the palatoquadrate of the *Amphibia* in general, and of the *Anura* in particular, present a number of problems regarding the homologies of the constituent parts. These problems cannot be finally solved unless the development, and especially the early development, of the chondrocrania of a large number of genera has been worked out. It is important that the development of the palatoquadrate and

sound-conducting apparatus be investigated in forms with a direct mode of development. As far as I am aware it has been done in the case of *Leiopelma* only, and this form lacks a plectrum.

The bulk of the work on the development of the anuran skull was done towards the end of the nineteenth century, mainly by Parker, Huxley, Goette, Stöhr and Gaupp. Gaupp's work on the development of the chondrocranium of *Rana esculenta* has for many years been accepted as applicable to all *Anura*. KRUIJTZER (1931) describing the development of the chondrocranium of *Megalophrys* (*Megophrys*) *montana* developed the theory that the attachment of the anuran jaws is of the hyostylic type. Two years later KOTTHAUS (1933) published his account of the development of the chondrocranium of *Xenopus laevis*. This was followed by descriptions of the development of the mandibular arch of *Rana temporaria* (PUSEY, 1938), the chondrocranium of *Calyptocephalus* (REINBACH, 1939), the chondrocranium of *Ascaphus truei* (VAN EEDEN, 1951), the chondrocranium of *Leiopelma* (N. G. STEPHENSON, 1951), the jaws of Bufo (SEDRA, 1950) and the sound-conducting apparatus of Bufo (BARRY, 1956).

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The following problems have been considered in the course of these investigations: the real nature of the otic process, the pterygoid process and the palatobasal connexion, and the homologies of the constituent parts of the sound-conducting apparatus.

The most convenient way of carrying out these investigations would have been to consider, in order of their appearance in time, a phylogenetic series of primitive amphibians and their larvae, which led up to the modern forms and thus attempt to discover the origin and history of the remarkable peculiarities which characterize the development of the palatoquadrate and sound-conducting apparatus of modern *Anura*. If such a procedure were possible it would have been necessary at each stage to pay attention to the functional significance of the constituent parts, as structure and function are always correlated. Unfortunately we know nothing of the larvae of the early amphibians, and our knowledge of the adults is practically restricted to the bony skull. Paleontological evidence alone cannot, therefore, be expected to prove the homologies of all the cartilaginous structures present in the neurocranium and in the viscerocranium of living tetrapods. On the other hand, there is no general agreement amongst comparative anatomists regarding the homologies of some of these structures.

More work remains to be done in this direction and many more developmental series of different kinds of anurans will have to be investigated before the picture becomes complete. Until further work has been undertaken some of the suggestions made in this paper regarding the homologies of the different structures investigated must, therefore, be considered as tentative.

Material and technique

The material used for these investigations consisted of a number of tadpoles in various stages of development, a few juvenile adults and a large adult female. They were collected in Jonkershoek near Stellenbosch where the type specimen of this genus was discovered by W. F. PURCELL. It was named *Heleophryne purcelli* by W. SCLATER (1898).

The material was fixed and preserved in 10 % and 4 % formaline respectively. The lenses were removed prior to microtomisation, and evisceration was carried out as far as possible. The younger specimens were decalcified in Ebner's fluid for about a week. All the larger specimens were transferred from the formaline solution directly to Müller's fluid. Except for the old adult skull, which was left in this fluid foı six weeks, the skulls were completely decalcified within three weeks. Bulk-staining in an alcoholic solution of Borax-carmine was carried out before the material was embedded in paraffin wax in the usual manner. The material was serially sectioned, either transversely or longitudinally, at 15 μ and counterstained on the slides with Heindenhain's Azan solution.

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Acknowledgements

I wish to record my thanks to the Council for Scientific and Industrial Research for financial assistance without which it would have been difficult to complete this research. I would also like to express my gratitude to the Board of Trustees of the National Zoological Gardens, Pretoria, which granted me study leave for this purpose and for putting a research microscope at my disposal. I am grateful to Dr. J. H. Skinner for preparing three series of sections of metamorphosing stages of *Heleophryne*.

This investigation was carried out under the supervision of Professor C. A. du Toit whom I wish to thank for his constructive criticism and advice in the preparation of this paper. I am also very grateful to Professor C. G. S. de Villiers for his personal interest and valuable criticism.

Description of the developmental stages

Stage 1 (Figs. 1—12)

External features: total length 22.3 mm.; length from tip of snout to vent 11.8 mm.

The floor of the neurocranium

The parachordals and trabeculae are already fused with each other and the membrane stretching across the fenestra hypophyseos is invaded by a single layer

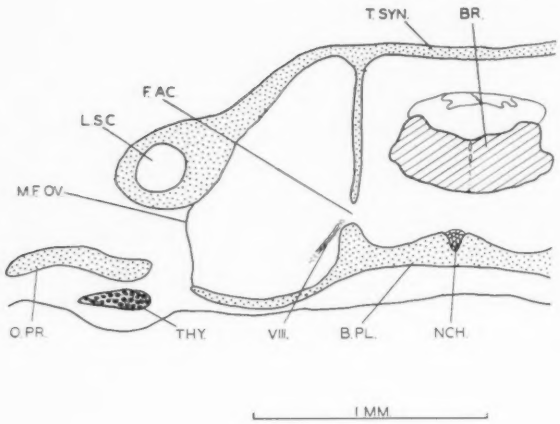

Fig. 1. Stage 1. Transverse section through the fenestra ovalis. B. PL., basal plate; BR., brain; F. AC., foramen acusticum; L.S.C., lateral semicircular canal; M.F.OV., membrana fenestrae ovalis; NCH., notochord; O.PR., otic process; THY., thymus; T.SYN., tectum synoticum; VIII., acoustic nerve.

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of cartilage cells. The paired carotid arteries and their palatine branches are enclosed, each in its own foramen, in the usual anuran manner. The flat intertrabecular plate is continuous with the broad ethmoidal plate in front.

The notochord can be traced up to the level of the anterior acoustic foramen. Its anterior end is covered by a thick cartilaginous hyperchordal bridge whereas its ventral surface abuts against the thin developing parasphenoid. Passing backwards the notochord becomes embedded in the basal plate until in the hinder region of the latter it is only ventrally covered by cartilage (Fig. 1). The course of the notochord in the posterior region of the basal plate in larval *Heleophryne* corresponds, therefore, with that of *Urodela* (DE BEER, 1937) and *Leiopelma archeyi* (E. M. STEPHENSON, 1951). However, as DE BEER (1937, p. 382) points out, these variations "are of little value for the estimation of phylogeny and affinity".

The side-wall of the neurocranium

The side-wall of the neurocranium is already fully chondrified. At the anterior end of the brain-case, which incidentally is closed by cartilage in front, the side-wall is pierced by the foramen olfactorium (Fig. 2). The oculomotor foramen is separated from the large optic foramen in front of it by a relatively broad pila metoptica (Fig. 8). The ophthalmic artery leaves the brain-case through its own foramen which is separated from the oculomotor foramen above it by a cartilage bar ("supratrabecular bar" of DE BEER, 1937?). The trochlear nerve has its own foramen high up in the orbital cartilage dorsally to the optic foramen (Fig. 8). As in the majority of *Anura* the prefacial commissure is absent and the foramen prooticum is a relatively large vertical opening between the otic capsule behind and the pila antotica in front.

A small cartilaginous rod projects ventro-laterad and slightly caudad from the

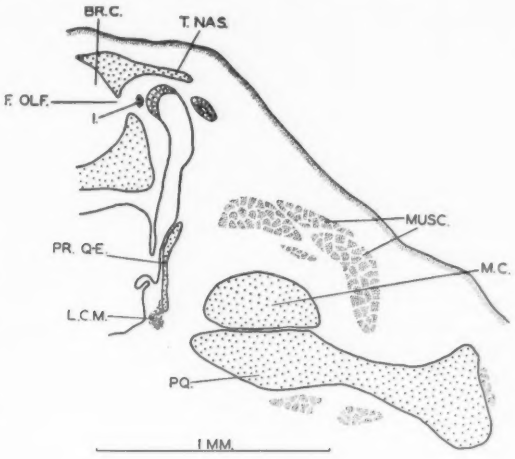

Fig. 2. Stage 1. Transverse section through the olfactory foramen. BR.C., brain cavity; F.OLF., olfactory foramen; L.C.M., ligamentum cornu-quadratum mediale; M.C., Meckel's cartilage; MUSC., muscles; PQ., palatoquadrate; PR.Q-E., processus quadrato-ethmoidalis; T.NAS., tectum nasi; 1., olfactory nerve.

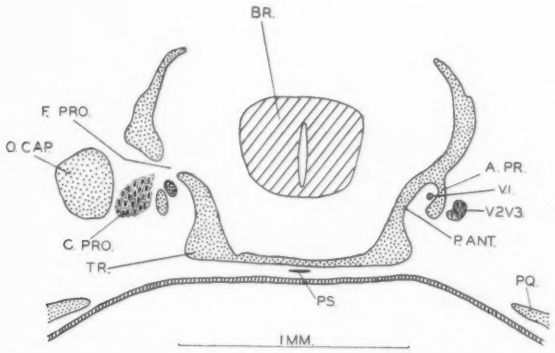

Fig. 3. Stage 1. Transverse section through the pila antotica. A.PR., dorsal vestige of the ascending process; BR., brain; F.PRO., foramen prooticum; G.PRO., prootic ganglionic mass; O.CAP., otic capsule; P.ANT., pila antotica; PQ., palatoquadrate; PS., parasphenoid; TR., trabecula; V.1., profundal nerve; V2V3., common ganglionic root of the mandibullar and maxillary nerves.

dorsal end of the pila antotica. Since the profundus V passes forward ventromedially to it and the r. maxillaris and r. mandibularis V dorso-laterally to it, this rod of cartilage bears all the relations to the branches of the n. trigeminus as a true processus ascendens palatoquadrati (Fig. 3). I therefore regard is as the dorsal vestige of a processus ascendens. It can reasonably be assumed that the ontogenesis of the palatoquadrate follows the usual anuran pattern, and that at this stage the ventral part of the processus ascendens is already destroyed.

The otic capsule

The otic capsule is already well developed and fused with the parachordal region of the neurocranium.

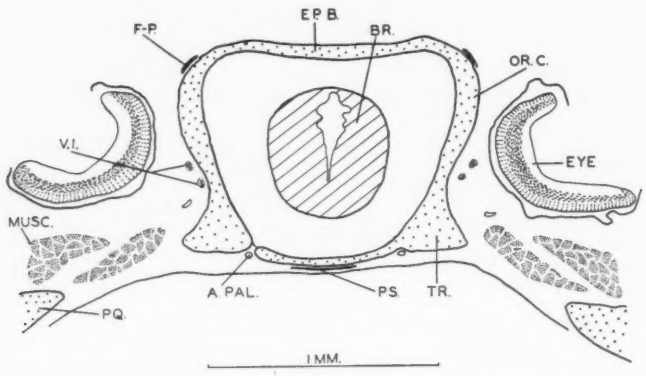

Fig. 4. Stage 1. Transverse section through the epiphyseal bar. A.PAL., palatine artery; BR., brain; EP.B., epiphyseal bar; F-P., frontoparietal; MUSC., muscle; OR.C., orbital cartilage; PQ., palatoquadrate; PS., parasphenoid; TR., trabecula; V.1., profundal nerve.

The lateral wall of the otic capsule is pierced by the fenestra ovalis which is closed by a thin membrane (Fig. 1). As yet, there is no trace of either an operculum or a columella. Dorsally to the fenestra ovalis the side-wall of the lateral semicircular canal forms a horizontal ridge-like bulge, the larval crista parotica, considered by some to be a derivative of the otic capsule, and by others to be a fused larval otic process. The available specimens were too far advanced in development to afford any conclusive evidence in favour of either of these two theories.

The vertical medial wall of the otic capsule, which forms the lateral wall of the brain-case in this region, is pierced, from in front backwards, by the following foramina: the foramen acusticum anterius which is separated from the foramen acusticum posterius by a thin strut of cartilage; the foramen endolymphaticum, which is situated dorsally to the foramen acusticum anterius; the foramen perilymphaticum superius, and, the foramen perilymphaticum inferius.

The roof of the neurocranium

The otic capsules are connected dorsally by a fairly broad tectum synoticum with which may be fused a tectum posterius (Fig. 6). A thin cartilaginous rod which connects the orbital cartilages dorsally halfway along their length is the epiphysial bar (Figs. 4 & 6). A taenia tecti medialis and taenia tecti transversalis are both absent.

The anterior end of the neurocranium and the suprarostral apparatus

The trabeculae are interconnected by an extensive ethmoidal plate, the anterolateral projections of which probably represent the trabecular horns. In the region

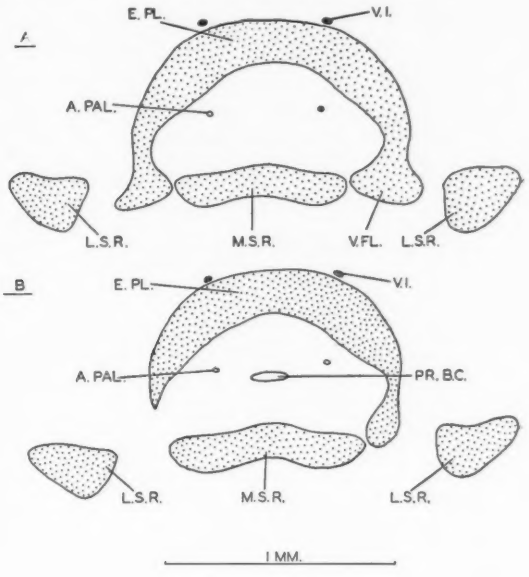

Fig. 5. A and B. Stage 1. Consecutive transverse sections through the anterior portion of the suprarostral. A.PAL., palatine artery; E.PL., ethmoidal plate; L.S.R. lateral wing of the suprarostral; M.S.R., medial portion of the suprarostral; PR.B.C., preoral buccal cavity; V.FL., ventral flange of the ethmoidal plate; V.1. profundal nerve.

of the suprarostral cartilage each trabecula gives rise to a ventral flange that ends ventrally in a broader "foot-plate" (Fig. 5).

The suprarostal cartilage is a heavily-built transverse structure supporting the preoral part of the larval sucker. From its anterior surface two deep U-shaped notches are cut out in such a manner that the suprarostral consists of a large median portion and two rod-like lateral wings (Fig. 7). The "foot-plates" of the trabecular flanges come to lie in these U-shaped notches. A tunnel is thus formed between the median portion of the suprarostral ventrally, the ethmoidal plate dorsally, and the trabecular flanges laterally. The lateral wings of the suprarostral articulate with the lateral edges of the "foot-plates" and are loosely connected to it by ligaments. The anterior part of the pre-oral buccal cavity lies in the posterior part of the tunnel (Fig. 5 B). A rather similar tunnel housing the preoral buccal cavity was described by PUSEY (1943) and VAN EEDEN (1951) for *Ascaphus*. In *Ascaphus,* however, the suprarostral consists of a large median plate and two separate lateral wings. Moreover, the median plate is fused with the trabecular flanges instead of articulating with them as in Heleophryne. Dorsally on the postero-lateral aspect of each lateral wing of the suprarostral is an independent triangular cartilage, the dorsal rostral (RAMASWAMI, 1944) (Figs. 6, 7 & 8).

The front wall of the brain-case is formed by a pair of pilae ethmoidales, situated immediately in front of the olfactory nerves and interconnected by a broad nasal septum which is confluent with the ethmoidal plate in front. Behind each olfactory nerve is situated the preoptic root of the orbital cartilage. The

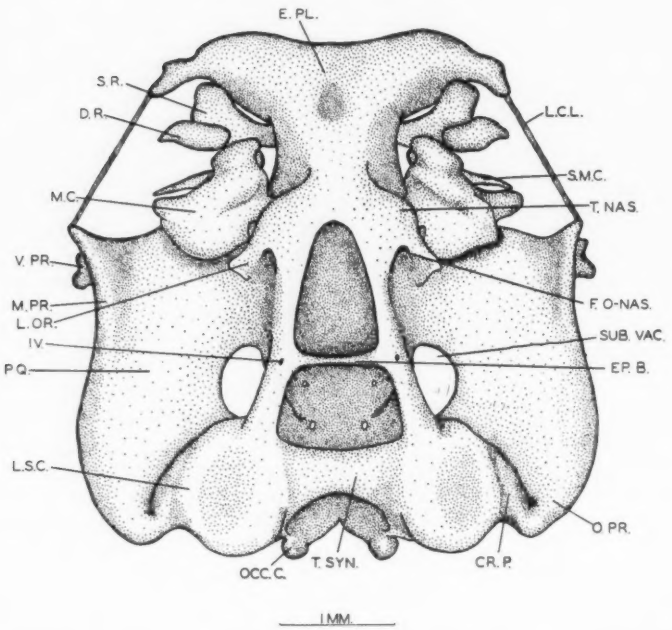

Fig. 6. Stage 1. Graphic reconstruction of the chondrocranium. Dorsal aspect. CR.P., parotic crest; D.R., dorsal rostral; EP.B., epiphyseal bar; E.PL., ethmoidal plate; F. O-NAS., orbitonasal foramen; L.C.L. ligamentum cornu-quadratum laterale; L.OR., lamina orbitonasalis; L.S.C., lateral semicircular canal; M.C., Meckel's cartilage; M.PR., muscular process; OCC.C.,occipital condyle; O.PR., otic process; PQ., palatoquadrate; S.M.C., sub-meckelian cartilage; S.R., suprarostral; SUB.VAC., subocular vacuity; T.NAS., tectum nasi; T.SYN., tectum synoticum; V.PR., ventral process of the palatoquadrate; IV., trochlear nerve.

dorsal ends of the latter are joined to the pilae ethmoidales in front by means of the sphenoseptal commissures.

The rod-like lamina orbitonasalis is connected dorsally to the anterior end of the orbital cartilage by a sphenethmoid commissure, thus forming the orbitonasal foramen through which the medial nasal branch of the n. profundus leaves the orbit and enters the nasal cavity. In front of the lamina orbitonasalis the sphenoseptal commissure and the hinder portion of the septum nasi are continued on each side into a relatively narrow tectum nasi (Fig. 6).

The palatoquadrate and its processes

The palatoquadrate is a very broad, flat plate of cartilage running laterally to, and more or less parallel to, the cranial floor. Passing forward from the posterior wall of the otic capsule it slopes gently downward so that its anterior tip lies well below the level of the cranial floor (Figs. 6 & 7). The anterior end of the palatoquadrate reaches forward to a point just behind the infrarostral

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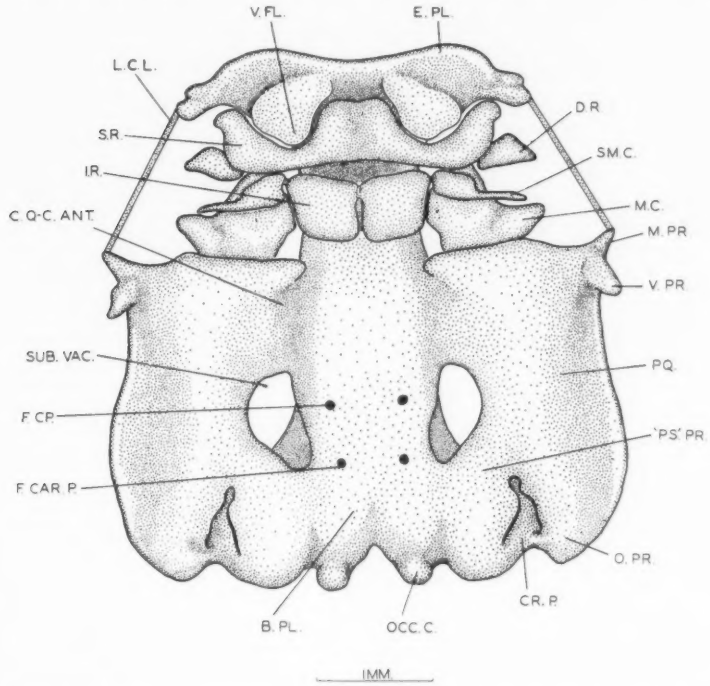

Fig. 7. Stage 1. Graphic reconstruction of the chondrocranium. Ventral aspect. B.PL., basal plate; C.Q-C.ANT., commissura quadratocranialis anterior; CR.P., crista parotica; D.R., dorsal rostral; E.PL., ethmoidal plate; F.CAR.P., foramen caroticum primarium; F.CP., cranio-palatine foramen; I.R., infrarostral; L.C.L., ligamentum cornu-quadratum laterale; M.C., Meckel's cartilage; M. PR., muscular process; OCC.C., occipital condyle; O.PR., otic process; PQ., palatoquadrate; 'PS'.PR., larval "pseudobasal" process; SM.C., submeckelian cartilage; S.R., suprarostral; SUB.VAC., subocular vacuity; V.FL., ventral flange of the ethmoidal plate; V.PR., ventral process of the palatoquadrate.

cartilage and is connected to the lateral wing of the ethmoidal plate by the ligamentum cornu-quadratum laterale.

The pars articularis palatoquadrati, as, in fact, the whole palatoquadrate has a more backward position than in *Rana temporaria* (Gaupp, 1896; Pusey, 1938), *Pelobates* (Dugès, 1834; Schultze, 1892; Luther, 1914), *Alytes* (van Seters, 1922), *Bombina* (Litzelmann, 1923) and *Calyptocephalus* (Reinbach, 1939) and projects only slightly beyond the anterior border of the commissura quadratocranialis anterior (Fig. 7).

The processus muscularis is only weakly developed as in *Ascaphus* (Pusey, 1943; van Eeden, 1951), the "Cystignathid" tadpole (Ramaswami, 1944), *Uperodon, Microhyla ornata* (Ramaswami, 1940) and *Xenopus* (Kotthaus, 1933; Paterson, 1939). Ventrally to the processus muscularis the palatoquadrate gives

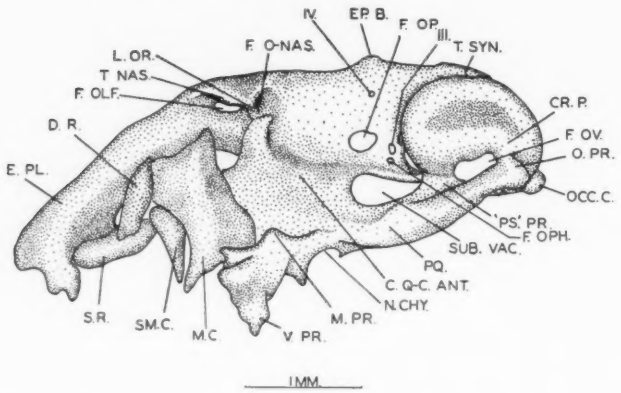

Fig. 8. Stage 1. Graphic reconstruction of the chondrocranium. Lateral aspect. C.Q-C.ANT., commissura quadrato-cranialis anterior; CR.P., crista parotica; D.R., dorsal rostral; EP.B., epiphyseal bar; E.PL., ethmoidal plate; F.OLF., foramen olfactorium; F.O-NAS., foramen orbitonasale; F.OP., foramen opticum; F.OPH., foramen for the ophthalmic artery; F.OV., fenestra ovalis; L.OR., lamina orbitonasalis; M.C., Meckel's cartilage; M.PR., muscular process; N.CHY., notch for the ceratohyal; OCC.C, occipital condyle; O.PR., otic process; PQ., palatoquadrate; 'PS'.PR., larval "pseudobasal" process; SM.C., submeckelian cartilage; S.R., suprarostral; SUB.VAC., subocular vacuity; T.NAS., tectum nasi; T.SYN., tectum synoticum; V.PR., ventral process of the palatoquadrate; III., oculomotor foramen; IV., trochlear foramen.

off a small but prominent ventrally directed process, the processus ventralis (Ramaswami, 1944).

The palatoquadrate is firmly anchored to the larval chondrocranium by means of three well-developed cartilaginous processes. These are, from in front backwards, the commissura quadrato-cranialis anterior, the processus "pseudobasalis" (basalis) and the processus oticus (Fig. 7).

The commissura quadrato-cranialis anterior

Near its anterior end the inner border of the palatoquadrate is suspended from the trabecular region of the neurocranial floor by the commissura quadrato-cranialis anterior. As in *Ascaphus* (Pusey, 1943; van Eeden, 1951) the commissura is very broad. In front it supports the posterior border of the choana and behind it reaches as far back as the anterior border of the optic foramen. Its anterior perpendicular portion forms a right angle with the cranial floor, while cross-sections through its hinder part reveal that it gradually slants sideways so that the angle between it and the cranial floor becomes bigger. The hind border of the commissure slowly curves backwards into the subocular shelf which projects ventro-laterad from the ventro-lateral edge of the trabecula. Passing backwards the subocular shelf becomes less conspicuous until it finally disappears in the region of the pila antotica.

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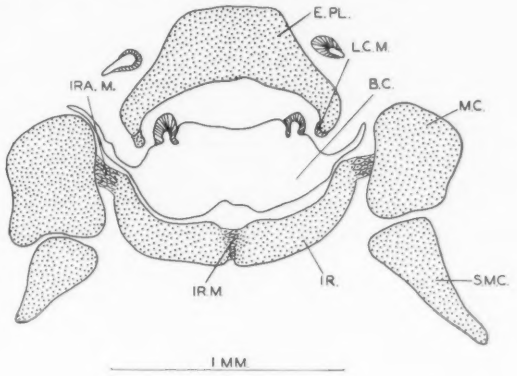

Fig. 9. Stage 1. Transverse section through the infrarostrals. B.C. buccal cavity; E.PL., ethmoidal plate; IR., infrarostral; IRA.M., intramandibular; IR.M. intermandibular; L.C.M., ligamentum cornu-quadratum mediale; M.C., Meckel's cartilage; S.M.C., submeckelian cartilage.

The processus quadrato-ethmoidalis is a small process projecting forwards from the anterior edge of the commissura quadrato-cranialis anterior (Fig. 8). A ligament, the ligamentum cornu-quadratum mediale passes forwards from this process to the ventral flange of the ethmoidal plate (Fig. 9).

The larval "pseudobasal" (basal) process

In the anterior region of the otic capsule immediately behind the prootic foramen the palatoquadrate establishes a connexion with the capsular floor and with the basal plate. The r. palatinus VII passes downwards in front of this process whereas the r. hyomandibularis VII runs backwards and downwards over it and then descends. According to DE BEER (1926) it is not a true basal connexion but an attachment to the neurocranium involving a postpalatine commissure for which the term "pseudobasal process" is more appropriate.

The larval "pseudobasal process" is broad and stretches between the hind border of the foramen prooticum and the front edge of the fenestra ovalis (Fig. 7).

The larval otic process

Behind the "pseudobasal" process the palatoquadrate passes backwards to the level of the posterior wall of the otic capsule. Near its posterior tip the dorsomedial part of the palatoquadrate is fused with the larval crista parotica which projects sideways as a ledge from the capsular wall postero-dorsally to the fenestra ovalis. This connexion between the palatoquadrate and the crista parotica is the larval otic connexion (Figs. 6, 7, 8 & 10).

The posterior end of the palatoquadrate projects some distance beyond the otic connexion and is connected by a thick ligament, the quadrato-otic ligament (RAMASWAMI, 1944), to the ventral wall of the otic capsule (Fig. 11).

In a younger larva of *Heleophryne* (total length 19.7 mm., length of head and trunk 8.1 mm.) the posterior end of the palatoquadrate reaches backward only

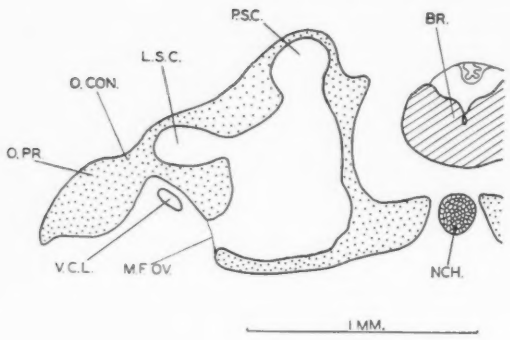

Fig. 10. Stage 1. Transverse section through the otic connexion. BR., brain; L.S.C., lateral semicircular canal; M.F.OV., membrana fenestrae ovalis; NCH., notochord; O.CON., otic connexion; O.PR., otic process (larval); P.S.C., posterior semicircular canal; V.C.L., vena capitis lateralis.

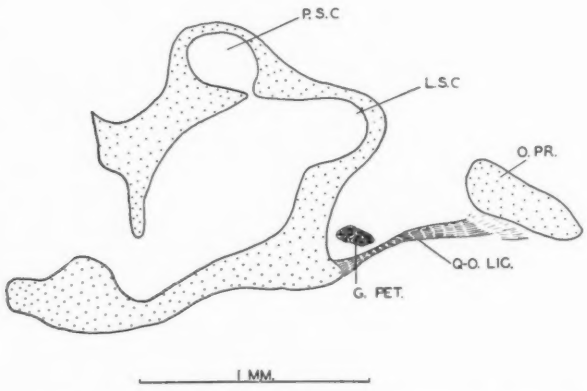

Fig. 11. Stage 1. Transverse section through the quadrato-otic ligament. G.PET., ganglion petrosum; L.S.C., lateral semicircular canal; O.PR., otic process; P.S.C., posterior semicircular canal; Q-O.LIG., quadrato-otic ligament.

as far as the crista parotica. The projection of the palatoquadrate behind the otic connexion is conspicuously absent and the medio-dorsal surface of the palatoquadrate abuts against the latero-ventral side of the crista parotica with which it has already started to fuse. The point of fusion, however, is still clearly indicated by intervening perichondrium.

In the majority of the *Anura* so far investigated the otic process is attached to the wall of the lateral semicircular canal, well in front of the fenestra ovalis. In *Heleophryne,* however, the point of attachment lies dorsally and postero-dorsally to the hind region of the fenestra. This condition seems to indicate that Pusey's interpretation of the larval otic attachment of *Ascaphus* is correct. I cannot agree with VAN EEDEN (1951, pp. 65—66) that Pusey's interpretation cannot be accepted because "the point of fusion concerned lies far behind the r. hyomandibularis VII, the a. orbitalis and the larval processus basalis, thereby lacking at least some of the fundamental relations of a true processus oticus. Its attachment,

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in toto, laterally to the fenestra ovalis instead of the usual one well in front of it also seems to negative Pusey's conclusions". According to its definition, the processus oticus itself and not its point of fusion with the otic capsule bears certain relations to the nerves and bloodvessels of that region. I can see no reason why the otic process must always fuse with the lateral semicircular canal "well in front" of the fenestra ovalis. Its position relative to the nerves and bloodvessels of this region seems to indicate that that portion of the palatoquadrate which lies behind the basal process represents the larval otic process.

The processus ascendens

RAMASWAMI (1944) reported the absence of a processus ascendens in larval *Heleophryne*. In 1938 he also reported its absence in *Philautus variabilis* but noted that earlier stages than the ones he had studied could not be obtained. Coming across what was presumably the same phenomenon he states that "Now, since it is absent in Heleophryne I am able to say definitely that the processus ascendens is not so uniformly met with as was previously thought be" (1944, p. 361). The chondocranium of the youngest larva of *Heleophryne* studied by RAMASWAMI (1944) was already well-developed (total length 27 mm.) and as he did not have younger stages at his disposal his conclusions cannot be accepted.

In the youngest larvae microtomised by me (also in one in which the hind limbs were already 16.5 mm. long) a small cartilaginous rod projects ventro-laterad and slightly caudad from the dorsal end of the pila antotica (Fig. 3). The distal end of this rod comes to lie at the base of the prootic ganglionic mass. The r. profundus V passes forward medially, and the r. maxillaris V and r. mandibularis V run forward dorso-laterally to it. Since it possesses all the relations to the branches of the trigeminal nerve of a true processus ascendens, I regard it as the dorsal vestige of a processus ascendens that breaks down early during the ontogeny although no traces of the supposed ventral fusion with the palatoquadrate have been found.

The ligaments of the palatoquadrate

Three ligaments, the quadrato-otic ligament (RAMASWAMI, 1944), the ligamentum cornu-quadratum mediale (SCHÜLZE, 1882) [= ligamentum quadrato-ethmoidalis of Gaupp)] and the ligamentum cornu-quadratum laterale (SCHÜLZE, 1882) [= trabecular-quadrate ligament of PUSEY (1938)] are attached to the larval palatoquadrate.

The quadrato-otic ligament

In addition to its otic connexion, the hind end of the larval palatoquadrate (pr. oticus) is connected to the floor of the otic capsule by means of a strong ligament, the quadrato-otic ligament (RAMASWAMI, 1944) (Fig. 11).

The ligamentum cornu-quadratum mediale

This ligament runs forward from the lower edge of the processus quadrato-ethmoidalis to the ventral flange of the ethmoidal plate (Fig. 9). According to PUSEY (1943) and VAN EEDEN (1951) a similar ligament in *Ascaphus* stretches from the lower edge of the commissura quadrato-cranialis anterior to the line of fusion of the trabecular flange with the median suprarostral plate.

The ligamentum cornu-quadratum laterale

From the antero-lateral tip of the palatoquadrate the ligamentum cornu-quadratum laterale passes forwards to the antero-lateral border of the ethmoidal plate (Fig. 7). As in *Rana* (PUSEY, 1938) it is independent of the suprarostrals. In *Ascaphus,* according to PUSEY (1943) and VAN EEDEN (1951), it is attached to the lateral wing of the suprarostral.

The lower jaw

As in other *Anura* the larval lower jaw in *Heleophryne* is composed of two pairs of cartilages: the paired infrarostrals (anterior jaw cartilages of Pusey) and the paired Meckel's cartilages (posterior jaw cartilages of Pusey).

Meckel's cartilage is a very heavily-built structure, and its most striking feature is, perhaps, its great rostro-caudad extension. Near its posterior end, it has a prominent ventro-laterally directed process (Fig. 8).

A club-shaped cartilage, the sub-Meckelian cartilage (RAMASWAMI, 1944), articulates with the ventral surface of Meckel's cartilage near its anterior end and supports the postero-lateral portion of the sucker (Figs. 7, 8 & 9). *Heleophryne* is the only anuran studied so far that has these cartilages.

The infrarostrals are two large, horizontal, more or less square plates that support the sucker behind the mouth opening (Fig. 9). Posteriorly the infrarostrals are held together by connective tissue, the histological character of which is that of procartilage; anteriorly they are interconnected by a cartilaginous bar (Fig. 7). The square-cut outer edge of each infrarostral abuts against the ventro-medial surface of the corresponding Meckel's cartilage. Anteriorly, however, an intramandibular of the nature of fibrocartilage forms a more rigid connexion between the two structures.

The Eustachian tube

The anlage of the Eustachian tube is a small rod-like outgrowth of the epithelium of the dorso-lateral portion of the pharynx. It is situated ventrally to the palatoquadrate, and opposite the "pseudobasal" process of the latter (Fig. 12).

Stage 2 (Figs. 13—15)

External features: early metamorphic stage; total length 59.8 mm.; length from tip of snout to vent 19.4 mm.; length of hind legs 16.5 mm.

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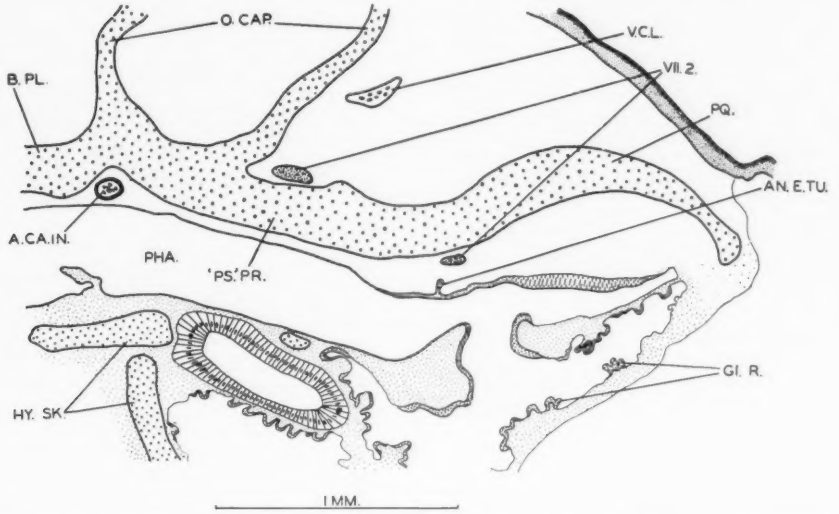

Fig. 12. Stage 2. Transverse section through the larval "pseudobasal" process. A. CA.INT. internal carotid artery; AN.E.TU., anlage of the Eustachian tube; B.PL., basal plate; GI.R., gill rakes; HY.SK., hyobranchial skeleton; O.CAP., otic capsule; PHA., pharynx; PQ., palatoquadrate; 'PS'.PR., larval "pseudobasal" process; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

The neurocranium has greatly increased in size since the previous stage. Although the constituent cartilages of the different regions show a general increase in size the most important advances concern the nasal and otic regions.

The floor of the neurocranium

There are no important advances to be reported in this region. However, the floor has thickened considerably, especially in the region of the former fenestra hypophyseos. The notochord, although much reduced, can still be traced up to the level of the posterior acoustic foramen. The hypochordal bridge is much thicker than in the previous stage.

The side-wall of the neurocranium

The side-wall has become more massive but it shows no structural changes. The "dorsal vestige of the processus ascendens" is still present in this stage although it is already absent in specimens slightly older than that of stage 1.

The otic capsule

The postero-medial part of the otic capsule and the postero-lateral regions of the basal plate and tectum synoticum are invaded by the ossifying exoccipital. The foramen perilymphaticum inferius is already enclosed in bone, and the ossi-

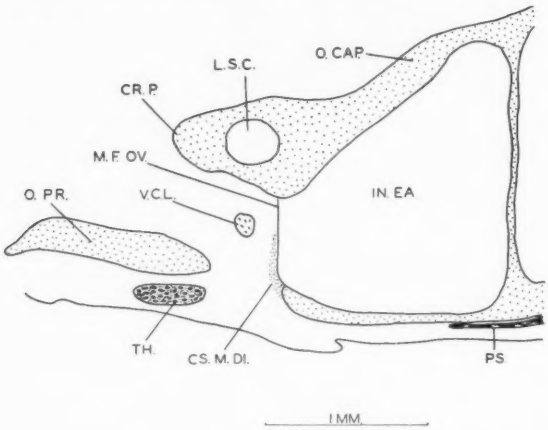

Fig. 13. Stage intermediate between stage 1 and stage 2. Transverse section through the fenestra ovalis. GR.P., crista parotica; CS.M.DI., cells forming mesenchymatous disk; IN.EA., inner ear; L.S.C., lateral semicircular canal; M.F.OV., membrana fenestrae ovalis; O.CAP., otic capsule; O.PR., otic process; PS., parasphenoid; TH., thymus; V.C.L., lateral head vein.

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fication reaches as far forward as the posterior border of the foramen perilymphaticum superius. The prootic which makes its appearance in a larva slightly older than that in which the exoccipital appears, is already fairly well-developed in this stage. It has spread into the anterior wall of the otic capsule and along the inner wall of the latter up to the anterior rim of the foramen acusticum anterius.

The fenestra ovalis and the sound-conducting apparatus

In developmental stages intemediate between stages 1 and 2 mesenchymatous cells accumulate on the outer surface of the membrana fenestrae ovalis. These cells seem to be liberated mainly from the lateral surface of the ventral edge of the fenestra ovalis (Fig. 13). A small operculum has made its appearance in the posterior part of this mesenchymatous mass at a point about equidistant from the dorsal and ventral rims of the fenestra (Fig. 14). The operculum is still relatively small and composed of very young cartilage. The plectrum has not yet made its appearance.

The roof of the neurocranium

The perichondral ossifications of the occipital arches, the exoccipitals, have now invaded the postero-lateral regions of the tectum synoticum.

The anterior end of the neurocranium and the suprarostral apparatus

The suprarostral and dorsal rostral cartilages have increased in size. The main progress made at this stage concerns the development of the nasal capsules. The

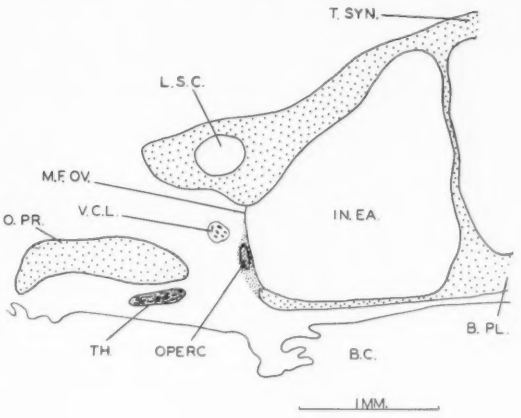

Fig. 14. Stage 2. Transverse section through the fenestra ovalis. B.C., buccal cavity; B.PL. basal plate; IN.EA., inner ear; L.S.C., lateral semicircular canal; M.F.OV., membrana fenestrae ovalis; OPERC., operculum; O.PR., otic process; TH., thymus; T.SYN., tectum synoticum; V.C.L., lateral head vein.

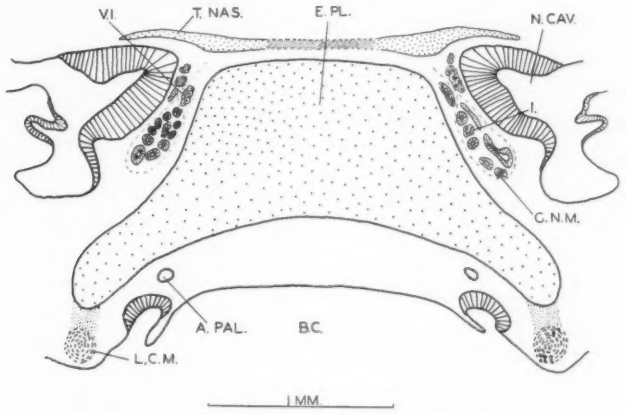

Fig. 15. Stage 2. Transverse section through the developing tectum nasi. A.PAL., palatine artery; B.C., buccal cavity; E.PL., ethmoidal plate; G.N.M., medial nasal gland; L.C.M., ligamentum cornu-quadratum mediale; N.CAV., nasal cavity; T.NAS., developing tectum nasi; 1., olfactory nerve; V.1., profundal nerve.

narrow tectum nasi of the previous stage has broadened considerably by the addition of young cartilage along its lateral edges. It has also grown forwards as a horizontal plate of cartilage lying dorsally to, and unconnected with, the latero-dorsal edge of the ethmoidal plate (nasal septum) (Fig. 15). In the angle between the developing tectum nasi and the septum nasi runs the median nasal branch of the profundus nerve.

The cartilago obliqua has started to chondrify, and the future cartilago alaris and most other constituent parts of the adult nasal capsule are either in the procartilaginous or in the mesenchymatous stage of development. The future cartilago praenasalis superior is faintly indicated in the mesenchymatous tissue

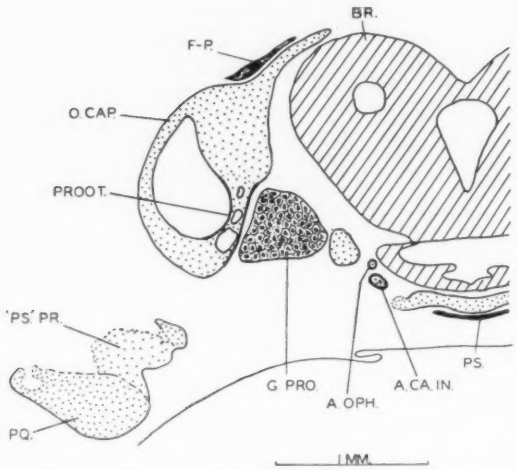

Fig. 16. Stage 3. Transverse section through the common foramen for the internal carotid and ophthalmic arteries. A.CA.IN., internal carotid artery; A.OPH., ophthalmic artery; BR., brain; F-P., fronto-parietal; G.PRO., prootic ganglionic mass; O.CAP., otic capsule; PQ., palatoquadrate; PROOT., prootic bone; PS., parasphenoid; 'PS'.PR., remnant of larval "pseudobasal" process.

but no traces of the future cartilago praenasalis inferior could be found. The effective floor of the nasal capsule at this stage, as in the previous one, is formed by the ethmoidal plate.

The palatoquadrate and its processes, and the lower jaw

The constituent cartilages of these structures show a general increase in size, but their general form and relations have remained unaltered.

The Eustachian tube

The anlage of the Eustachian tube has grown forward ventrally to the palatoquadrate, and its anterior end lies opposite the pila antotica.

Stage 3 (Figs. 16—21)

External features: total length 57.9 mm.; length from tip of snout to vent 26 mm. Hind and front legs present in a relatively well developed condition; horny tooth-blades in process of disappearance.

Compared with the preceding stages this larva shows advances in nearly all the regions of the neurocranium and of the viscerocranium. These are particularly pronounced in the more anterior regions of the neurocranium where they are intimately connected with the change in mode of life of the animal at metamorphosis.

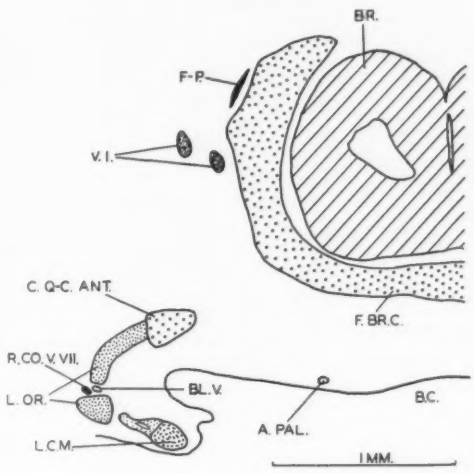

Fig. 17. Stage 3. Transverse section through the developing lamina orbitonasalis. A.PAL., palatine artery; B.C., buccal cavity; BL.V., boodvessel; BR., brain; C.Q-C.ANT., commissura quadrato-cranialis anterior; F.BR.C., floor of the brain-case; F-P., frontoparietal; L.C.M., ligamentum cornu-quadratum mediale; L.OR., lamina orbitonasalis; R.CO.V.VII., ramus communcans between nerves V and VII; V.I., profundal nerve.

The floor of the neurocranium

The notochord is further reduced and reaches forward as far as the level of the foramen perilymphaticum superius.

The floor of the neurocranium has undergone considerable changes, especially in the trabecular region where the subocular ledge has been removed from the lateral edge of the trabecula by the process of perichondral erosion. Anteriorly, the medial uneroded part of the trabecula still forms the ventro-lateral wall of the neurocranium. Posteriorly, in the region of the foramina for the internal carotid and ophthalmic arteries, the destruction has been more extensive, and on the left side these foramina have become confluent as a result of the erosion of the intervening trabecular cartilage (Fig. 16). On the right side these arterial foramina are still separated by a narrow strut of partly eroded cartilage. Furthermore, the floor of the brain-case, laterally to the parasphenoid, shows signs of perichondral erosion along its ventral aspect. The connexion of the commissura quadrato-cranialis anterior with the trabecula has been destroyed almost entirely and only a narrow portion along its anterior edge is still uneroded and intact (Fig. 17).

The side-wall of the neurocranium

The whole orbital cartilage has undergone erosion, particularly along its outer aspect and in the regions of the optic and the ophthalmic foramina. The olfactory foramen has become enlarged by the erosion of its margins. The optic foramen has increased in size mainly by the erosion of its anterior and dorsal edges. Erosion along its posterior border has reduced the pila metoptica to a narrow cartilaginous pillar. Ventrally to the optic foramen the trabecula has

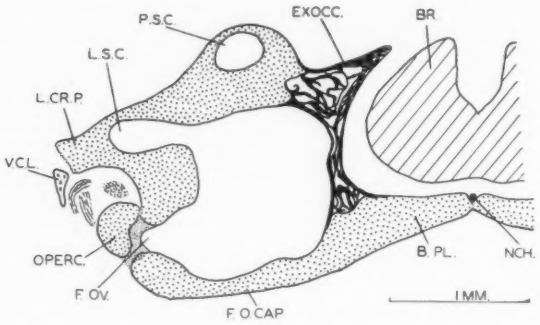

Fig. 18. Stage 3. Transverse section through the hinder portion of the fenestra ovalis. B.PL., basal plate; BR., brain; EXOCC., exoccipital; F.O.CAP., floor of otic capsule; F.OV., fenestra ovalis; L.CR.P., larval parotic crest; L.S.C., lateral semicircular canal; NCH., notochord; OPERC., operculum; P.S.C., posterior semicircular canal; V.C.L., lateral head vein.

undergone erosion along its dorsal, lateral and ventral aspects, and only a comparatively thin bar of (trabecular) cartilage still intervenes between the optic and cranio-palatine foramina. The ophthalmic foramen has also increased in size and, on the left side, destruction of the trabecular bar between it and the ventrally situated internal carotid foramen has led to the confluence of these two foramina. A narrow portion of the trabecula persists between these two foramina on the right side. The cartilaginous bridge between the ophthalmic and the oculomotor foramina is reduced to a thin cartilaginous rod. The dorsal vestige of the ascending process has disappeared from the pila antotica which shows signs of perichondral erosion along its lateral aspect.

The otic capsule

The exoccipital reaches to the anterior edge of the foramen perilymphaticum posterius. The latter is now enclosed in bone except for its antero-ventral edge which is still cartilaginous. The prootic shows a similar increase in size.

Dorsally to the posterior half of the fenestra ovalis the "larval" crista parotica from which the larval otic process has been eroded has a rough outer edge lacking a perichondrium (Fig. 18). The "adult" crista parotica has started to chondrify in front of the former "larval" parotic crest and appears as an outgrowth of the wall of the lateral semicircular canal. Although its juvenile cartilage is histologically distinguishable from the older cartilage of the latter, no perichondrium intervenes between them.

The fenestra ovalis and the sound-conducting apparatus

The operculum has grown considerably since the previous stage and now projects beyond the posterior rim of the fenestra ovalis where it is synchondrotically fused with the capsular side-wall. More anteriorly, the dorsal edge of the

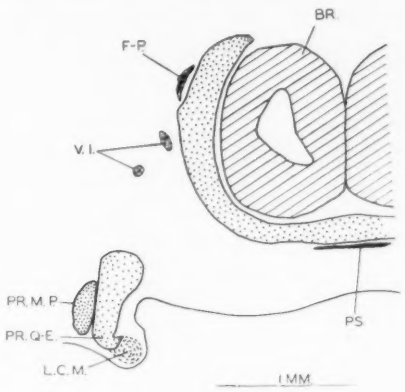

Fig. 19. Stage 3. Transverse section through the developing processus maxillaris posterior. BR., brain; F-P., fronto-parietal; L.C.M., ligamentum cornu-quadratum mediale; PR.M.P., processus maxillaris posterior; PR.Q-E., processus quadrato-ethmoidalis; PS., parasphenoid; V.1., branches of the profundal nerve.

operculum is in the process of fusing with the postero-dorsal rim of the fenestra (Fig. 18). The developing musculus opercularis is attached to the outer, convex surface of the now saucer-shaped operculum.

Between the antero-dorsal end of the operculum and the dorsal rim of the fenestra ovalis the pars interna plectri has made its appearance as a small nodule of very young cartilage in the mesenchymatous tissue of the membrana fenestrae ovalis. Anteriorly it becomes procartilaginous and merges into a tract of mesenchyme cells that passes forwards and ventro-laterad towards the Eustachian tube.

The crista praeopercularis has started to chondrify laterally on the ventral rim of the fenestra ovalis. It chondrifies in the same mesenchymatous tissue as does the pars interna plectri and consists of very young cartilage.

The roof of the neurocranium

No important advances have taken place in this region.

The anterior end of the neurocranium and the suprarostral apparatus

The advances shown in this region are many and amount to a considerable reduction and destruction of the original suprarostral structures and the greater part of the ethmoidal plate on the one hand, and to the rapid development of the nasal capsules on the other.

The dorsal rostrals have disappeared entirely. The lateral wings of the suprarostral have undergone enchondral destruction and their perichondria, or what remains of them, cover empty spaces. The median portion of the suprarostral also shows signs of enchondral destruction. Furthermore, its lateral edges as well as its median part show signs of intensive perichondral erosion. On each side the lateral wing of the ethmoidal plate together with the front part of the ligamentum cornu-quadratum laterale has disappeared.

In front of the anterior edge of the commissura quadrato-cranialis anterior the lateral plate-like portion of the lamina orbitonasalis has started to chondrify. Morphologically it lies laterally to the commissura and extends obliquely outward, downward and backward (Fig. 17). Its distal portion, which is pierced by a foramen for a small nerve and bloodvessel, bears two processes, a small processus maxillaris anterior and a stouter processus maxillaris posterior pointing forward and backward respectively. The processus maxillaris anterior ends freely in front, whereas the processus maxillaris posterior comes to lie against the lateral surface of the processus quadrato-ethmoidalis, being separated from it by the perichondrium of the latter (Fig. 19).

The constituent parts of the nasal capsule are already well chondrified. The cartilago praenasalis inferior has started to develop on the lateral surface of the ethmoidal plate in front of the "ventral flanges" and is in the process of fusing with the solum nasi. The latter develops as a horizontally situated lateral cartilaginous plate on the outer surface of the trabecular plate dorsally to the ventral flanges. Attached to the dorsally directed inner end of the solum is the well-developed crista intermedia with its lamina superior and lamina inferior. The latter is already fused with the planum terminale of the cartilago obliqua.

The palatoquadrate and its processes

As already mentioned (see otic capsule), the connexion of the larval otic process with the lateral surface of the lateral semicircular canal has been destroyed. The erosion has not only destroyed the otic connexion but also the entire hind end of the palatoquadrate (proc. oticus) behind the larval "pseudobasal" process. Even this latter process has undergone enchondral erosion but its perichondrium, although buckled, is more or less intact (Fig. 20).

The commisura quadrato-cranialis anterior has undergone destruction along its caudal edge so that only its front edge with the processus quadrato-ethmoidalis remains intact. As a result of the backward rotation of the palatoquadrate which is already in progress, the commissura has rotated backwards about its point of attachment to the brain-case and now forms an acute angle with the floor of the latter. Meanwhile the posterior end of the developing processus maxillaris posterior has come to lie against the lateral surface of the processus quadrato-ethmoidalis (Fig. 19).

As a result of the backward rotation of the palatoquadrate and its simultanious backward displacement, it has attained a more vertical position and now forms an acute angle of approximately 40 degrees with the base of the skull. Its hind end occupies a position alongside the front wall of the otic capsule, whereas its articular region lies in the orbital region. Perichondral erosion has set in along the dorso-alteral edge of the palatoqudrate. Its processus muscularis and processus ventralis are being destroyed enchondrally and their perichondria have folded back onto the dorsal and ventral surfaces of the palatoquadrate respectively.

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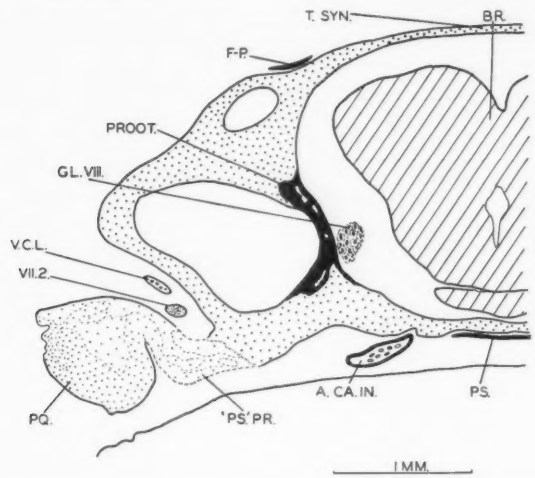

Fig. 20. Stage 3. Transverse section through the larval "pseudobasal" process. A. CA.IN., internal carotid artery; BR., brain; F-P., fronto-parietal; GL.VIII., ganglion acusticum; PQ., palatoquadrate; PROOT., prootic; PS., parasphenoid; 'PS'.PR., remnant of the larval "pseudobasal" process; T.SYN., tectum synoticum; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

There is no buckling of the posterior part of the palatoquadrate as in *Rana* (Gaupp, 1892; Pusey, 1938) and *Bufo* (Barry, 1956).

The ligamentum cornu-quadratum mediale is still intact but the ligamentum cornu-quadratum laterale, especially its anterior end, has started to disintegrate.

The lower jaw

The two anterior jaw cartilages (infrarostrals) are still set transversely across the snout but are now more rod-like in appearance and each has started to fuse with the posterior jaw cartilage (Meckel's cartilage) of its side (Fig. 21). The posterior jaw cartilage has undergone reduction in so far as its processes have been eroded away. It has, however, gained in length and is at this early metamorphic stage a thick rod-like cartilage stretching between the lateral end of the anterior jaw cartilage and the anterior end of the pars articularis where a ball-and-socket joint has replaced the flat articular surfaces of the previous stage.

The sub-meckelian cartilages have disappeared completely.

The Eustachian tube

The anlage of the Eustachian tube has further increased in length, and its anterior end, in which a small lumen has made its appearance, lies ventro-laterally to the palatoquadrate in the region of the former ventral process.

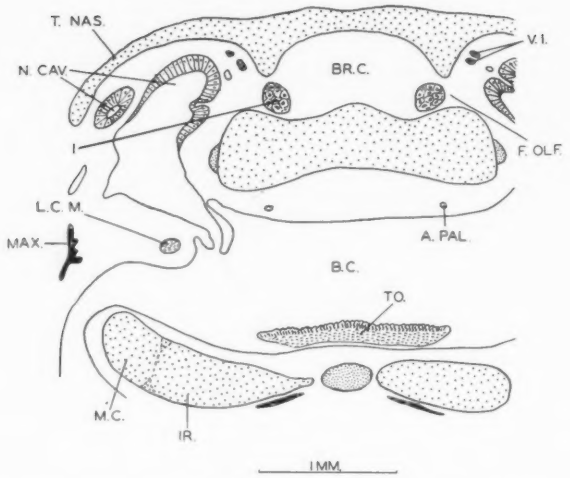

Fig. 21. Stage 3. Transverse section through the olfactory foramen. A.PAL., palatine artery; B.C., buccal cavity; BR.C., brain case; F.OLF., foramen olfactorium; IR., infrarostral (= anterior jaw cartilage); L.C.M., ligamentum cornu-quadratum mediale; MAX., maxillary; M.C., Meckel's cartilage (posterior jaw cartilage); N.CAV., nasal cavities; T.NAS., tectum nasi; TO., tongue; 1., olfactory nerve; V.1., profundal nerve.

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Stage 4 (Figs. 22—23)

External features: Total length 62.6 mm.; length from tip of snout to vent 22.7 mm.; legs well developed; corner of mouth ventrally to eye.

The floor of the neurocranium

The cranial portion of the notochord has undergone further degeneration and is now reduced to a slender rod which lies in a shallow middorsal groove in the posterior part of the basal plate. Anteriorly it still reaches forward to the level of the foramen perilymphaticum posterius.

The notch between the exoccipital condyles has become deeper as a result of the posterior part of the hypochordal bridge being perichondrally eroded away from behind.

The cartilaginous (trabecular) bridge between the foramina for the internal carotid and ophthalmic arteries on either side has been completely destroyed.

The side-wall of the neurocranium

The foramen opticum shows a further increase in size. The pila metoptica has been resorbed so that the foramina for the optic and oculomotor nerves have become confluent. The cartilage bridge between the former foramen oculomotorium and the foramen for the ophthalmic artery (the latter foramen now confluent with the internal carotid foramen) is still intact (Fig. 22). The same

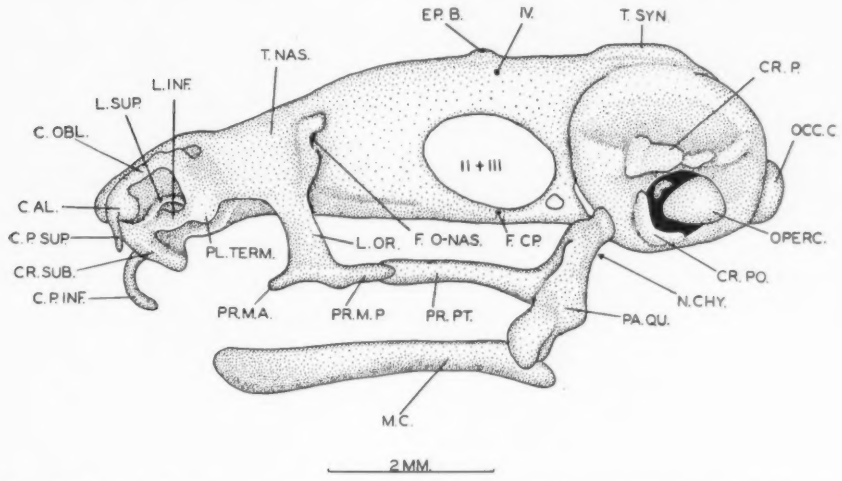

Fig. 22. Stage 4. Graphic reconstruction of the chondrocranium. Lateral aspect. C.AL., cartilago alaris; C.OBL., cartilago obliqua; C. P.INF., cartilago praenasalis inferior; C.P.SUP., cartilago praenasalis superior; CR.P., crista parotica; CR.PO., crista praeopercularis; CR.SUB., crista subnasalis; EP.B., epiphyseal bar; F.CP., cranio-palatine foramen; F.O-NAS., foramen orbitonasale; L.INF., lamina inferior; L.OR., lamina orbitonasalis; L.SUP., lamina superior; M.C., lower jaw; N.CHY., notch for the ceratohyal; OCC.C., occipital condyle; OPERC., operculum; PA.QU., pars quadrata; PL.TERM., planum terminale; PR.M.A., processus maxillaris anterior; PR.M.P., processus maxillaris posterior; PR.PT., processus pterygoideus; T.NAS., tectum nasi; T.SYN., tectum synoticum; II +III., foramen for the optic and oculomotor nerves; IV., trochlear foramen.

applies to the cartilage bridge between the optic foramen and the now very small cranio-palatine foramen.

The otic capsule

The exoccipital has further increased in extent and reaches forward to the level of the foramen acusticum posterius. The foramen perilymphaticum superius is now enclosed in bone.

The adult crista parotica has increased in size and forms a ledge of young cartilage along the outer face of the lateral semicircular canal, dorsally to the anterior half of the fenestra ovalis. Behind the developing adult crista parotica the larval crista parotica still shows a rough outer edge where the larval otic process has been eroded away.

Ventrally to the posterior part of the operculum the latero-dorsal surface of the capsular floor is now lined with a thin layer of juvenile cartilage. This becomes thicker in later stages, loses its juvenile character, and forms a cartilaginous ridge along the ventral rim of the fenestra ovalis in the young adult.

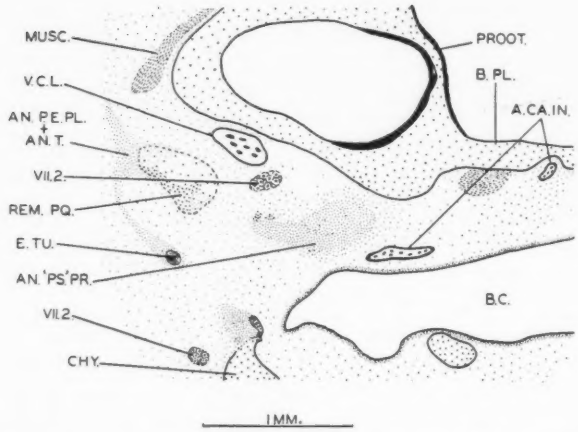

Fig. 23. Stage 4. Transverse section through the anlage of the adult "pseudobasal" process. A.CA.IN., internal carotid artery; AN.P.E.PL+AN.T., mesenchymatous anlage of the pars externa plectri and the anulus tympanicus; AN.'PS'.PR., anlage of the adult "pseudobasal" process; B.C., buccal cavity; B.PL., basal plate; CHY., ceratohyal; E.TU., Eustachian tube; MUSC., muscle; PROOT., prootic; REM.PQ., remnant of the palatoquadrate; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

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The sound-conducting apparatus

The operculum has increased in size, mainly by the addition of young cartilage along its outer, ventral and anterior borders (Fig. 22).

The cartilaginous anlage of the pars interna plectri has also increased in size and, as in the preceding stage, its procartilaginous anterior end merges into a strand of mesenchyme. This mesenchymatous strand, the anlage of the pars media plectri, passes outward towards the dorsal aspect of the Eustachian tube, and continues antero-dorso-laterad to a point laterally to the eroded hind end of the palatoquadrate. Here it merges into the formative tissue of the pars externa plectri and anulus tympanicus which is formed by the accumulation of cells liberated from the hind end of the larval palatoquadrate (Fig. 23).

The mesenchymatous anlage of the pars media plectri passes outward towards the Eustachian tube and the r. hyomandibularis VII runs backward over it.

The crista praeopercularis now reaches forward to a point immediately in front of the fenestra ovalis where its dorsally directed anterior end which is still procartilaginous, lies mesially to the procartilaginous anterior (distal) tip of the pars interna plectri (Fig. 22). There is as yet no cartilaginous connexion between the crista praepercularis and the pars interna plectri.

The roof of the neurocranium

The cartilaginous roof of the nerocranium shows no marked advances over that of the previous stage.

The Chondrocranium of Heleophryne Purcelli Sclater

The anterior end of the neurocranium and the suprarostral apparatus

Almost all the constituent cartilages of the nasal capsules have now made their appearance, and their general arrangement is similar to that of the juvenile described by DU TOIT (1933). Anteriorly, the nasal septum is broad and flat and projects beyond the nasal capsules.

The suprarostral cartilage as well as the ventral flanges of the ethmoidal plate have been destroyed and the connexion of the commissura quadrato-cranialis anterior with the antero-lateral surface of the neurocranium has been severed.

The palatoquadrate and its processes

The three (or four?) larval connexions of the palatoquadrate with the neurocranium have now been destroyed. The processus maxillaris posterior of the lamina orbitonasalis has increased in length and the inner surface of its posterior end is fused with the outer face of the processus quadrato-ethmoidalis. The processus maxillaris posterior thus forms the anterior end of the developing processus pterygoideus of the palatoquadrate (Fig. 22). Along the inner side of the pterygoid process lies the remains of the much-eroded dorsal end of the former commissura quadrato-cranialis anterior.

The palatoquadrate has become more erect and forms an acute angle of approximately 60°—65° with the longitudinal axis of the skull. Its dorsal end lies lateral to the antero-ventro-lateral surface of the otic capsule without being in cartilaginous contact with it.

The perichondral erosion and destruction of the hind end of the palatoquadrate are still in progress and have now reached the notch for the ceratohyal.

A cloud of loosely packed cells that stretches from the medial side of the pars quadrata to the anterolateral side of the capsular floor is the formative tissue of the adult "pseudobasal" process (Fig. 23). These cells occupy the same position as the larval "pseudobasal" process of younger stages and they are presumably derived from it.

As a result of the destruction of the ventral flanges of the ethmoidal plate the ligamentum cornuquadratum mediale has become detached in front, and its fibres have begun to disintegrate in this region. Posteriorly it is still intact and runs forward from the tip of the processus quadrato-ethmoidalis along the inner surfaces of the posterior and anterior maxillary processes.

The lower jaw

The fusion between the anterior and posterior jaw cartilages of each side is now an intimate one. The jaw as a whole has increased in length and the articular region has come to lie under the optic foramen. In the articular region juvenile cartilage has been added onto its dorsal, medial and hind surfaces, as well as onto the ventral and lateral surfaces of the articular facet of the palatoquadrate.

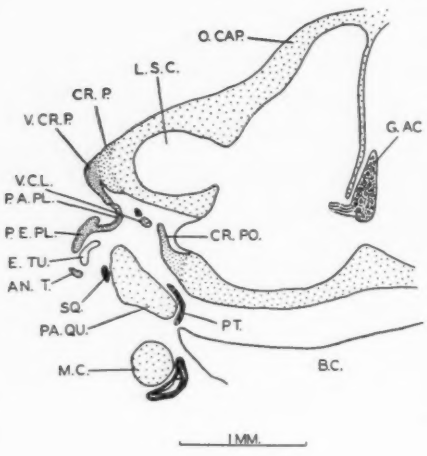

Fig. 24. Stage 5. Transverse section through the anterior portion of the fenestra ovalis. AN.T., anulus tympanicus; B.C., buccal cavity; CR.P., crista parotica; CR.PO., crista praeopercularis; E.TU., Eustachian tube; C.AC., ganglion acusticum; L.S.C., lateral semicircular canal; M.C., lower jaw; O.CAP., otic capsule; PA.QU., pars quadrata; P.A.PL., processus ascendens partis externae plectri; P.E.PL., pars externa plectri; PT., pterygoid bone; SQ., squamosum; V.C.L., lateral head vein; V.CR.P., visceral portion of the parotic crest.

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The Eustachian tube

The anterior end of the Eustachian tube has been displaced backward and lies opposite the pila antotica.

Stage 5 (Figs. 24—27)

External features: total length 22.6 mm.; length from tip of snout to vent 18.1 mm.; corner of mouth ventrally to otic capsule.

The floor of the neurocranium

The chondrocranial portion of the notochord has disappeared and the perichondral erosion along the border of the inter-condylar notch has ceased.

The side-wall and roof of the neurocranium

These regions are similar to those of stage 4 and no noteworthy changes are to be reported.

The otic capsule

The ossification of the exoccipital and prootic has not advanced as far as in stage 4.

The adult parotic crest is slightly larger than in stage 4, and its lateral portion seems to be derived, at least partly, from the cartilage cells set free by the breaking down, during early metamorphosis, of the larval otic process and the posterior end of the larval palatoquadrate (Fig. 24). Its antero-lateral portion has started to grow forward and is slightly bent downward towards the postero-dorsal end of the palatoquadrate without coming in cartilaginous contact with it. Near its anterior end the crista parotica gives off a small ventrally directed

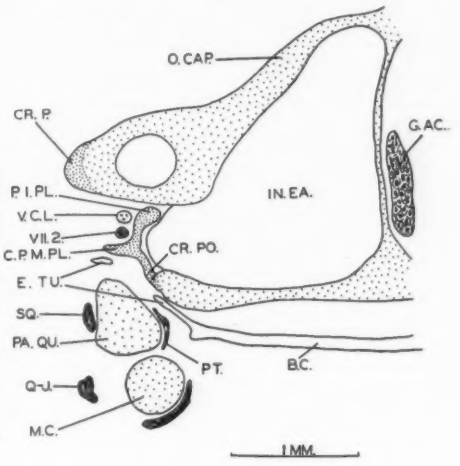

Fig. 25. Stage 5. Transverse section through the pars media plectri. B.C., buccal cavity; C.P.M.PL., cartilaginous precursor of the pars mediaplectri; CR.P., crista parotica; CR.PO., crista praeopercularis; E.TU., Eustachian tube; G.AC., ganglion acusticum; IN.EA., inner ear; M.C., lower jaw; O.CAP., otic capsule; PA.QU., pars quadrata; P.I.PL., pars interna plectri; PT., pterygoid; Q-J., quadrato-jugal; SQ., squamosum; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

procartilaginous process which merges into the dorsal tip of the mesenchymatous anlage of the processus ascendens partis externae plectri (Fig. 24).

The rough outer edge of the larval parotic crest has been smoothed out and has a more rounded appearance in cross-section. There is no thickening of the capsular floor in the posterior part of the fenestra ovalis as in stage 4. Immediately in front of the fenestra ovalis the anterior end of the crista praeopercularis fuses with a thin layer of juvenile cartilage that has been added on to the outer surface of the lateral wall of the otic capsule. This narrow strip of young cartilage stretches upward from its point of fusion with the crista praeopercularis to the base of the developing crista parotica (Fig. 29).

The sound-conducting apparatus

Compared with the preceding stage the operculum has not undergone any noteworthy changes.

The pars interna plectri has grown considerably and now forms a cartilaginous plug which fits into the gap between the dorsal rim of the fenestra ovalis and the dorsal edge of the crista praeopercularis. Its postero-dorsal end occupies a position mesial to the antero-dorsal end of the operculum whereas its ventral edge is now synchondrotically fused with the dorsal edge of the crista praeopercularis (Fig. 25). The procartilaginous anlage of the pars media plectri arises in continuity with the ventro-lateral surface of the anterior end of the pars interna plectri. As it passes out in a lateral direction towards the mesenchymatous anlage of the pars externa plectri, it lies dorsally to the Eustachian tube.

The anlage of the pars externa plectri, although still mesenchymatous, is now distinguishable from that of the anulus tympanicus. A mesenchymatous strand, which connects the ventro-medial aspect of the anlage of the pars externa plectri

with a ventrally directed procartilaginous process of the adult crista parotica, is the anlage of the processus ascendens partis externae plectri (Fig. 24).

The anulus tympanicus

As already mentioned, the mesenchymatous anlage of the pars externa plectri has become differentiated from that of the anulus tympanicus. The latter, which is crescent-shaped represents the postero-ventral, ventral and antero-ventral parts of the anulus. Although it is mesenchymatous for its greater part, procartilage has made its appearance in its antero-ventral portion.

The ramus hyomandibularis VII

After leaving the prootic ganglionic mass ventrally, the r. hyomandibularis passes dorso-lateral over the front face of the otic capsule and then backward over the developing processus "pseudobasalis" where it lies mesially to the lateral head vein (Fig. 23). Behind the "pseudobasal" process it passes backwards over the developing plectrum where the pars media plectri merges into the vertically situated pars interna plectri. Immediately behind the plectrum it is joined by the ramus communicans between VII and IX, then passes ventrally and devides into its main branches.

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The palatoquadrate and its processes

The processus pterygoideus has further increased in length and the processus quadrato-ethmoidalis is now indistinguishably fused with the posterior end of the processus maxillaris posterior. As a result of the lengthening of the processus pterygoideus the pars quadrata has moved backwards, especially its lower articular end, and now forms an obtuse angle of approximately 120 degrees with the longitudinal axis of the neurocranium. The dorsal end of the pars quadrata still lies sligthly in front of the anterior end of the developing crista parotica whereas its ventral articular end lies below and laterally to the fenestra ovalis (Fig. 26).

The "pseudobasal" process has started to chondrify and consists of juvenile cartilage. Its anterior inner end abuts against the floor of the otic capsule in front of the fenestra ovalis, whereas its lateral (distal) end is separated from the inner surface of the pars quadrata by a dorsally directed ridge of the pterygoid bone (Fig. 27 B). Dorsally to this bony ridge the antero-dorsal edge of the lateral end of the "pseudobasal" process has started to fuse with the pars quadrata (Fig. 27 A). In a slightly younger stage (total length 46.5 mm.; length from tip of snout to vent 19.6 mm.) there is no fusion between the "pseudobasal" process and the pars quadrata. Since these two structures are intimately fused in later stages of development, fusion probably takes place in a rostro-caudal direction.

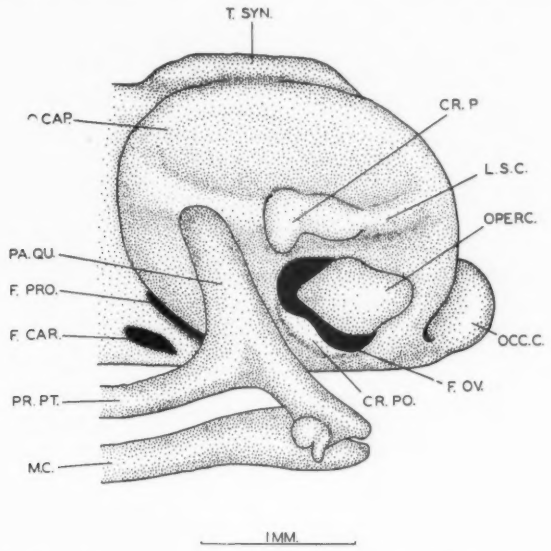

Fig. 26. Stage 5. Graphic reconstruction of the otic capsule and associated structures. Lateral aspect. (Plectrum deleted for the sake of clarity). CR.P., crista parotica; CR.PO., crista praeopercularis; F.CAR., common foramen for the internal carotid and ophthalmic arteries; F.OV., fenestra ovalis; F.PRO., foramen prooticum; L.S.C., lateral semicircular canal; M.C., lower jaw; O.CAP., otic capsule; OCC.C., occipital condyle; OPERC., operculum; PA.QU., pars quadrata; PR.PT., pterygoid process; T.SYN., tectum synoticum.

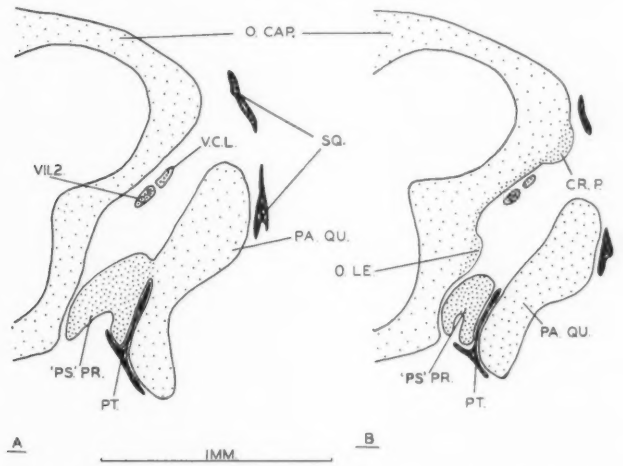

Fig. 27. A and B. Stage 5. Consecutive transverse sections through the developing adult "pseudobasal" process. CR.P., parotic crest; O.CAP., otic capsule; O.LE., otic ledge; PA.QU., pars quadrata; 'PS'.PR., "pseudobasal" process; PT., pterygoid; SQ., squamosum; V.C.L.,: lateral head vein; VII.2., hyomandibular nerve.

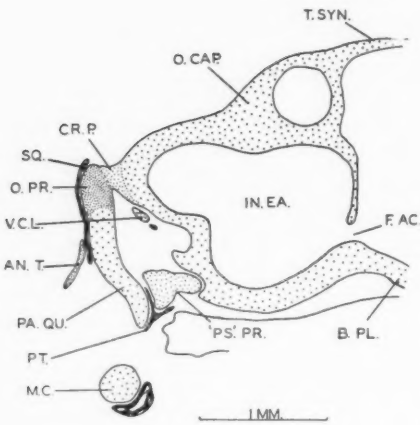

Fig. 28. Stage 6. Transverse section through the otic process. AN.T., anulus tympanicus; B.PL., basal plate; CR.P., parotic crest; F.AC., foramen acusticum; IN.EA., inner ear; M.C., lower jaw; O.CAP., otic capsule; O.PR., otic process; PA.QU., pars quadrata; 'PS'.PR., "pseudobasal" process; PT., pterygoid; SQ., squamosum; T.SYN., tectum synoticum; V.C.L., lateral head vein.

The lower jaw

The lower jaw has further increased in length and its articular ends lie ventrolaterally to the fenestra ovalis (Fig. 26). The cartilages of the lower jaw are now round in cross-section and the erosion of their surfaces has ceased.

The Eustachian tube

The Eustachian tube has shortened considerably and its anterior portion, which has moved backwards to the level of the prootic foramen, lies laterally to the pars quadrata.

Stage 6 (Figs. 28—33)

External feature: juvenile adult; length from tip of snout to vent 17 mm.; legs well developed; tail absent.

The floor and the side-wall of the neurocranium

The cranial portion of the notochord, in contrast with that of stage 5, is still present in the most posterior region of the basal plate where it lies in a shallow mid-dorsal groove.

Erosion of the floor and side-wall of the neurocranium has now ceased. The oculomotor and optic foramina are confluent as are the foramina for the internal carotid and ophthalmic arteries. The foramen for the trochlear nerve pierces the orbital cartilage dorsally to the optic foramen. The foramen craniopalatinum has disappeared.

The otic capsule

The adult parotic crest has expanded further, not only laterad but also in a caudo-rostral direction along the outer surface of the lateral semicircular canal.

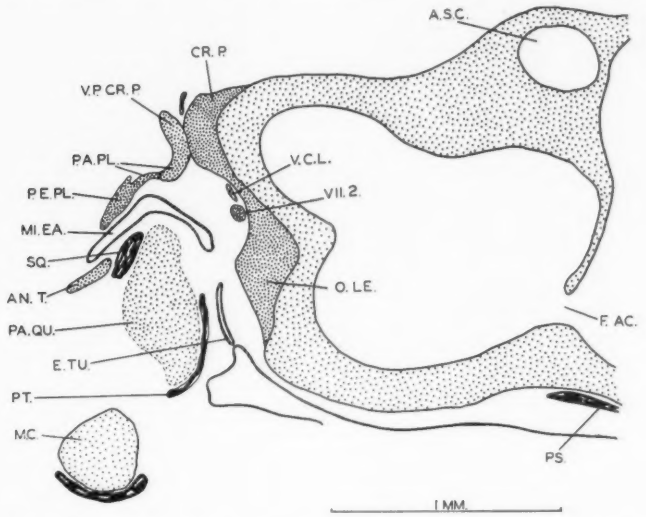

Fig. 29. Stage 6. Transverse section through the otic ledge and the pars externa plectri. AN.T., anulus tympanicus; A.S.C., anterior semicircular canal; CR.P., crista parotica; E.TU., Eustachian tube; F.AC., foramen acusticum; M.C., lower jaw; MI.EA., middle ear; O.LE., otic ledge; P.A.PL., processus ascendens partis externae plectri; PA.QU., pars quadrata; P.E.PL., pars externa plectri; PS., parasphenoid; PT., pterygoid; SQ., squamosum; V.C.L., lateral head vein; V.P.CR.P., visceral portion of crista parotica; VII.2., hyomandibular nerve.

Its distal portion, formed by the conversion of cartilage cells of the destroyed hind end of the larval palatoquadrate into cartilage, has grown forward and downward and is now synchondrotically fused with the postero-dorsal, dorsal and dorso-medial aspects of the pars quadrata (Fig. 28). The otic process thus formed is, therefore, not an outgrowth of the adult pars quadrata, but it is formed by the cartilage cells which were set free during the destruction of the hind end of the larval palatoquadrate (larval otic process of this paper).

Near its posterior end the distal portion of the parotic crest gives off a ventrally directed cartilaginous process that fuses with a dorsally directed procartilaginous process of the pars externa plectri (Fig. 29). The processus ascendens partis externae plectri is, therefore, of dual origin. Behind this process the lateral edge of the crista parotica is fused with the posterior arm of the anulus tympanicus (Fig. 30).

As in stage 5 a thin layer of juvenile cartilage connects the base of the parotic crest with the anterior end of the crista praeopercularis in front of the fenestra ovalis. At the point of junction a block of young cartilage, the otic ledge, has started to develop on the antero-lateral surface of the side-wall of the otic capsule immediately behind the developing processus "pseudobasalis" (Fig. 29).

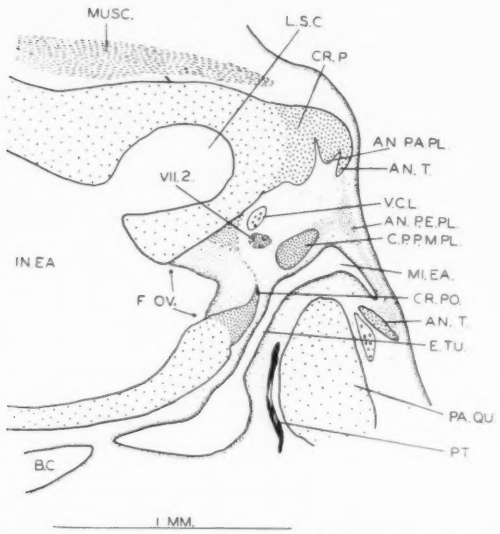

Fig. 30. Stage 6. Transverse section through the middle ear cavity. AN.P.A.PL., dorsal anlage of the processus ascendens partis externae plectri; AN.P.E.PL., mesenchymatous anlage of the pars externa plectri; AN.T., anulus tympanicus; B.C., buccal cavity; C.P.P.M.PL., cartilaginous precursor of the pars media plectri; CR.P., crista parotica; CR.PO., crista praeopercularis; E.TU., Eustachian tube; F.OV., fenestra ovalis; IN.EA., inner ear; L.S.C., lateral semicircular canal; MI.EA., middle ear; MUSC., muscle; PA.QU., pars quadrata; PT., pterygoid; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

The exoccipital and the prootic bones are in more or less the same stage of development as those of stage 4.

The sound-conducting apparatus

The operculum is similar to that of stage 5 but its antero-dorsal edge is now connected by procartilage to the lateral aspect of the postero-dorsal end of the pars interna plectri (Fig. 31).

The constituent parts of the plectrum are still either in the cartilaginous or in the procartilaginous state. Chondrification of the plectrum takes place in a proximo-distal direction.

As mentioned above the lateral surface of the postero-dorsal end of the pars interna plectri is connected by procartilage to the antero-dorsal surface of the operculum. Its antero-ventral edge is synchondrotically fused with the thin dorsal surface of the crista praeopercularis. Ventro-laterally to this connexion the ceratohyal is now synchondrotically fused with the lateral surface of the crista praeopercularis (Fig. 32). The precursor of the pars media plectri which was still procartilaginous in stage 5, is now fully chondrified. From the outer lower anterior surface of the pars interna plectri, the cartilaginous precursor of the pars media plectri passes in an antero-lateral direction and fuses with the dorsal inner

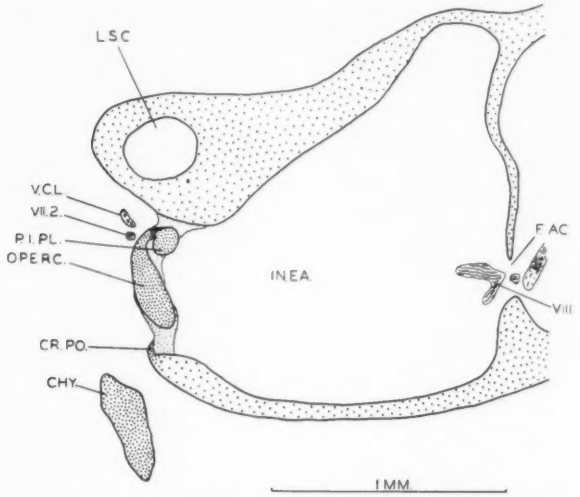

Fig. 31. Stage 6. Transverse section through the posterior end of the pars interna plectri. CHY., ceratohyal; CR.PO., crista praeopercularis; F.AC., foramen acusticum; IN.EA., inner ear; L.S.C., lateral semicircular canal; OPERC., operculum; P.I.PL., pars interna plectri; V.C.L., lateral head vein; VII.2., hyomandibular nerve; VIII., acoustic nerve.

face of the procartilaginous pars externa plectri (Fig. 30). Ventro-medially the disk-like pars externa plectri gives rise to a dorsally directed procartilaginous process which fuses with a ventrally directed cartilaginous process of the crista parotica to form the processus ascendens partis externae plectri (Fig. 29).

The anulus tympanicus

The anulus tympanicus consists of juvenile cartilage. It is sickle shaped, and the posterior arm is fused dorsally with the postero-lateral edge of the parotic crest (Fig. 30). The anterior arm is not yet fully developed, and there is a wide gap between its dorsal end and the parotic crest.

The palatoquadrate and its processes

The pars quadrata forms an obtuse angle of approximately 130—135 degrees with the longitudinal axis of the neurocranium. The pars quadrata, and especially its ventral articular end, has been displaced backwards as the result of the rostro-caudad lengthening of the processus pterygoideus. Meanwhile the lateral portion of the crista parotica has grown forward and downward, and the dorsal end of the pars quadrata has been pushed back onto its antero-ventral surface and has fused with it. The connexion thus formed is the adult otic connexion.

The "pseudobasal" process has elongated in a transverse direction, thus displacing the ventral articular portion of the pars quadrata laterally. The lateral end of the "pseudobasal" process is more extensively fused with the medial face of

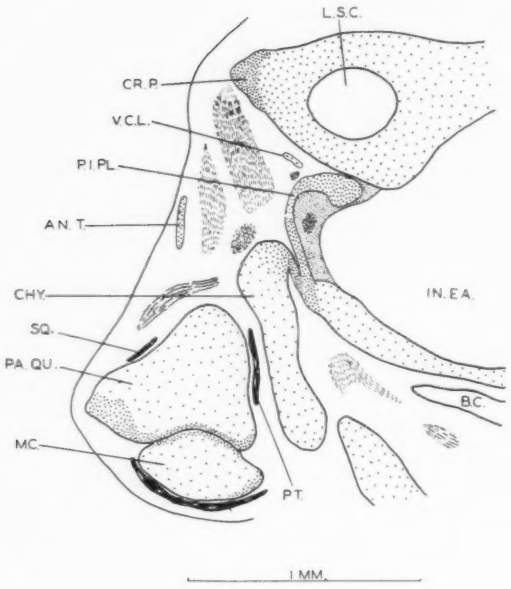

Fig. 32. Stage 6. Transverse section through the connexion of the ceratohyal to the crista praeopercularis. AN.T., anulus tympanicus; B.C., buccal cavity; CHY., ceratohyal; CR.P., crista parotica; IN.EA., inner ear; L.S.C., lateral semicircular canal; M.C., lower jaw; PA.QU., pars quadrata; P.I.PL., pars interna plectri; PT., pterygoid; SQ., squamosum; V.C.L. lateral head vein.

the pars quadrata above the dorsal ridge of the pterygoid bone. A layer of juvenile cartilage, added onto the medial surface of the pars quadrata, connects the outer end of the "pseudobasal" process with the distal ventral end of the otic process. This is the so-called "dorsal process" of the "pseudobasal" process.

The medial end of the "pseudobasal" process is directed slightly forward and fits into a shallow groove along the latero-ventral part of the front wall of the otic capsule. It lies opposite the prootic foramen, in front of the origin of the palatine and the hyomandibular nerves (Fig. 33).

The lower jaw

The lower jaw has more or less attained the adult condition.

The Eustachian tube

The Eustachian tube now occupies the adult position. Its lumen has increased in size, and its distal end has expanded into the tympanic cavity or the cavity of the middle ear (Figs. 29 & 30).

Stage 7 (Figs. 34—42)

External features: adult female; length from tip of snout to vent 49 mm.

This animal is obviously an old adult as can be judged from its large size and the extensive ossification in the different regions of the neurocranium.

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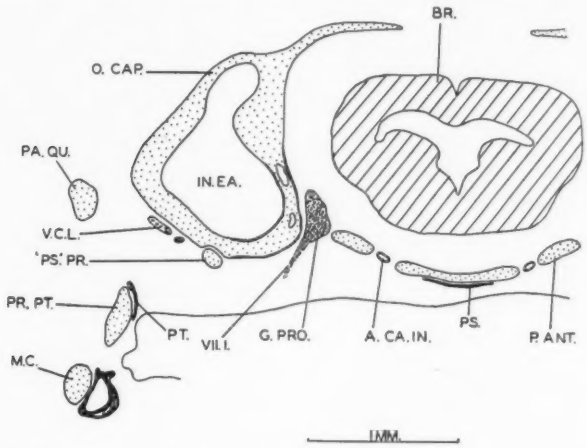

Fig. 33. Stage 6. Transverse section through the prootic ganglionic mass. A.CA.IN., internal carotid artery; BR., brain; G.PRO., prootic ganglionic mass; IN.EA., inner ear; M.C., lower jaw; O.CAP., otic capsule; P.ANT., pila antotica; PA.QU., pars quadrata; PR.PT., pterygoid process; PS., parasphenoid; 'PS'.PR., anterior end of "pseudobasal" process; PT., pterygoid; V.C.L., lateral head vein; VII.1., palatine nerve.

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The floor and side-wall of the neurocranium

The os en ceinture which will be described in detail in another section reaches backward to a point immediately in front of the optic foramen. Posteriorly, the exoccipital and prootic bones have invaded the lateral parts of the basal plate (Fig. 34). The side-wall of the neurocranium between the otic capsules and the os en ceinture remains cartilaginous except for the dorsal and ventral borders of the prootic foramen into which the prootic has extended. The foramina in the side-wall are the same as in the preceding stage.

The otic capsule

These are extensively ossified. Both the exoccipital and the prootic are large and are fused with each other. The prootic invades the side-wall of the neurocranium, reaches forward to the antero-dorsal rim of the prootic foramen, and also forms the posterior and postero-ventral borders of the latter. Furthermore, it has extended into the antero-lateral region of the basal plate, the antero-lateral portion of the tectum synoticum and the proximal half of the parotic crest (Fig. 35). The exoccipital ossification not only occupies the posterior half of the otic capsule, the postero-lateral region of the basal plate and of the tectum synoticum, but has also spread into the condyles; only the posterior, dorsal and ventral articular surfaces of the latter remain cartilaginous.

One of the most striking features of the otic capsule of the adult is the enormous parotic crest whose basal half is well ossified (Figs. 35—41). Distally it

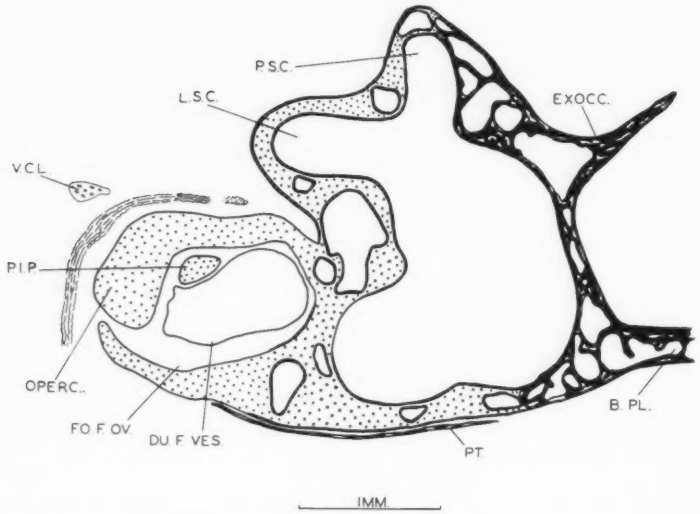

Fig. 34. Stage 7. Transverse section through the fossa fenestrae ovalis. B.PL., basal plate; DU.F.VES., ductus fenestrae vestibuli; EXOCC., exoccipital; FO.F.OV., fossa fenestrae ovalis; L.S.C., lateral semicircular canal; OPERC., operculum; P.I.P., pars interna plectri; P.S.C., posterior semicircular canal; PT., pterygoid; V.C.L., lateral head vein.

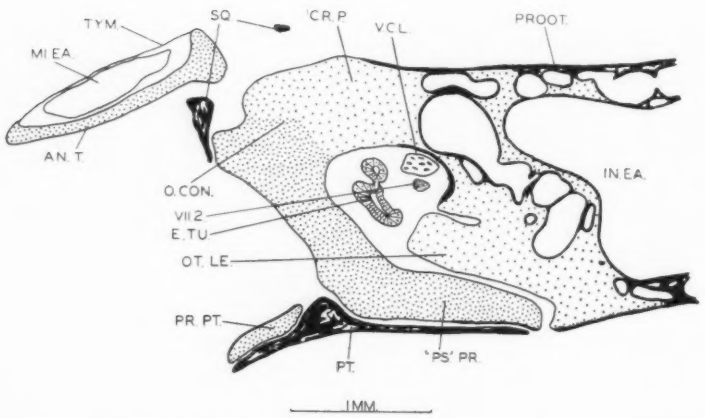

Fig. 35. Stage 7. Transverse section through the otic ledge. AN.T., anulus tympanicus; CR.P., crista parotica; E.TU., Eustachian tube; IN.EA., inner ear; MI.EA., middle ear; O.CON., otic connexion; OT.LE., otic ledge; PROOT., prootic; PR.PT., pterygoid process; 'PS'.PR., "pseudobasal" process; PT., pterygoid; SQ., squamosum; TYM., tympanum; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

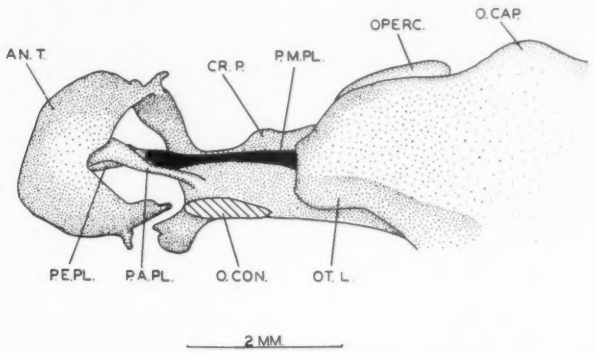

Fig. 36. Stage 7. Graphic reconstruction of the otic region. Ventral aspect. AN.T., anulus tympanicus; CR.P., crista parotica; O.CAP., otic capsule; O.CON., otic connexion; OPERC., operculum; OT.L., otic ledge; P.A.PL., processus ascendens partis externae plectri; P.E.PL., pars externa plectri; P.M.PL., pars media plectri.

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has developed an antero-laterally directed process that ends freely and a postero-lateral (postsquamosal) process that is fused with the dorsal end of the posterior arm of the anulus tympanicus (Figs. 36 & 37). The broad otic process and the more slender processus ascendens partis externae plectri are fused with the ventral surface of the parotic crest (Fig. 36).

Ventrally to the fenestra ovalis, the lateral edge of the capsular floor has grown out into a prominent laterally directed cartilaginous ledge which forms the floor of the fossa fenestrae ovalis (Figs. 34 & 38). This ledge projects backward beyond the fenestra ovalis along the side-wall of the otic capsule. In front of the operculum its dorsally directed outer edge, the crista praeopercularis, is synostotically fused with the ossified ventral edge of the pars interna plectri (Fig. 39). In front of the fenestra ovalis its anterior end merges into a block of cartilage, the otic ledge, whose ventral and anterior surfaces articulate with the dorsal and posterior surfaces of the medial end of the "pseudobasal" process (Fig. 35). This cartilaginous block (the otic ledge) has already started to develop in stage 5 in the region where a strip of young cartilage from the base of the parotic crest merges into the anterior end of the crista praeopercularis. The "pseudobasal" process chondrifies in front of the otic ledge, and with the backward movement and rotation of the pars quadrata it is moulded to fit closely over the anterior and ventral surfaces of the otic ledge.

As in the previous stages only two acoustic foramina are present in the adult.

The sound-conducting apparatus

As a result of the pronounced lateral extension of the floor of the fossa fenestrae ovalis, the ventral portions of the operculum and the pars interna plectri

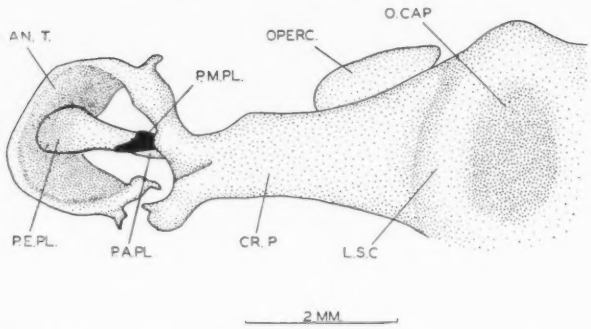

Fig. 37. Stage 7. Graphic reconstruction of the otic region. Dorsal aspect. AN.T., anulus tympanicus; CR.P., crista parotica; L.S.C., lateral semicircular canal; O.CAP., otic capsule; OPERC., operculum; P.A.PL., processus ascendens partis externae plectri; P.E.PL., pars externa plectri; P.M.PL., pars media plectri.

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have been displaced side-ways so that these two structures, which in previous stages have a vertical position, are now nearly horizontal (Figs. 34 & 38).

The operculum has increased in size, and the musculus opercularis is firmly inserted into its dorso-lateral surface. Its posterior portion projects backwards well beyond the posterior rim of the fenestra ovalis where it is accompanied on its ventral side by the ductus fenestrae vestibuli (Fig. 34).

The anterior end of the pars interna plectri is almost completely ossified and forms a bony plug in the anterior part of the fossa fenestrae ovalis. Its dorsal and postero-ventral borders, however, remain cartilaginous. The posterior portion of the pars interna plectri remains cartilaginous and projects backward along the ventral surface of the operculum to a point immediately behind the posterior border of the fenestra ovalis (Fig. 34). The antero-ventral edge of the pars interna plectri is synostotically fused with the dorsal bony edge of the crista praeopercularis (Fig. 39).

The proximal part of the cartilaginous precursor of the pars media plectri has become ossified, and it is impossible to determine the border between it and the pars interna plectri. Distally it is still cartilaginous and synchondrotically fused with the pars externa plectri. The latter part of the plectrum remains cartilaginous and is a more or less ovoid plate inserted into the tympanum. The pars media is continued into its dorsal part whereas its cartilaginous processus ascendens connects its medio-ventral surface with the parotic crest (Figs. 36, 37 & 38).

The anulus tympanicus is still sickle shaped with its posterior arm fused with the postero-lateral process of the parotic crest. The anterior arm of the anulus gives off a small process that is hooked around the squamosal from behind in such a way that it comes to lie between the latter and the antero-lateral process of the parotic crest (Figs. 36 & 37).

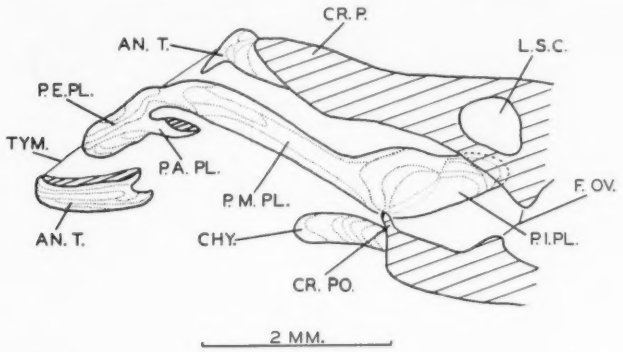

Fig. 38. Stage 7. Semi-diagrammatical reconstruction of the sound-conducting apparatus. Anterior aspect. AN.T., anulus tympanicus; CHY., ceratohyal; CR.P., crista parotica; CR.PO., crista praeopercularis; F.OV., fenestra ovalis; L.S.C., lateral semicircular canal; P.A.PL., processus ascendens partis externae plectri; P.E.PL., pars externa plectri; P.I.PL., pars interna plectri; P.M.PL., pars media plectri; TYM., tympanum.

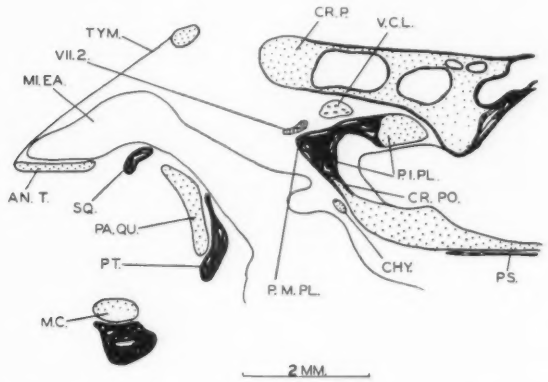

Fig. 39. Stage 7. Transverse section through the middle ear. AN.T., anulus tympanicus; CHY., ceratohyal; CR.P., crista parotica; CR.PO., crista praeopercularis; M.C., lower jaw; MI.EA., middle ear; PA.QU., pars quadrata; P.I.PL., pars interna plectri; P.M.PL., pars media plectri; PS., parasphenoid; PT., pterygoid; SQ., squamosum; TYM., tympanum; V.C.L., lateral head vein; VII.2., hyomandibular nerve.

The roof of the neurocranium

The lateral part of the tectum synoticum has been invaded from behind by the exoccipital and to a lesser extent from in front by the prootic. Its middorsal part remains cartilaginous.

The epiphysial bar which is already present in stage 1 persists into the adult (Fig. 41).

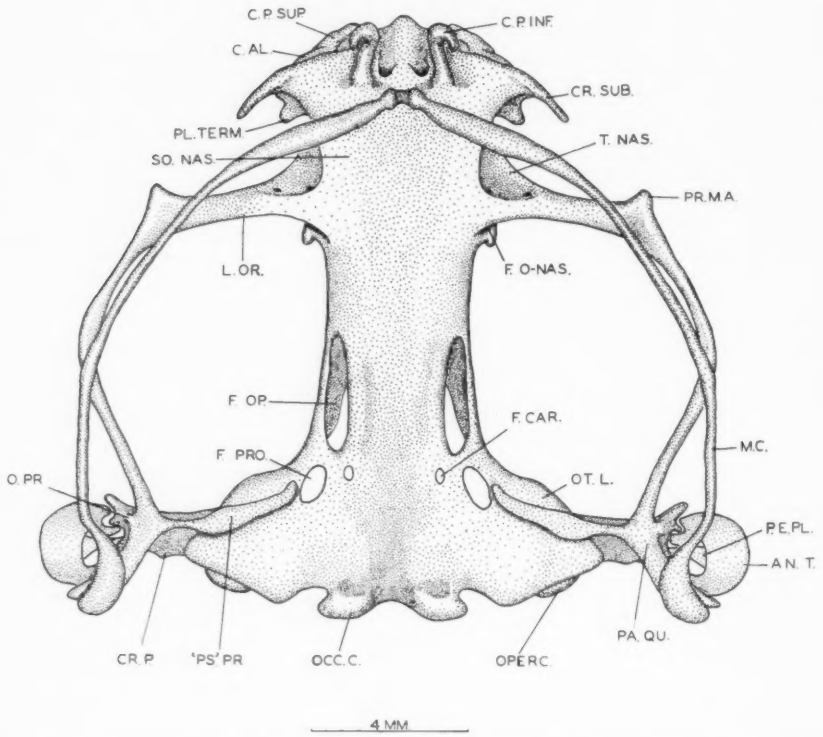

Fig. 40. Stage 7. Graphic reconstruction of the chondrocranium. Ventral aspect. AN.T., anulus tympanicus; C.AL., cartilago alaris; C.P.INF., cartilago praenasalis inferior; C.P.SUP., cartilago praenasalis superior; CR.P., crista parotica; CR.SUB., crista subnasalis; F.CAR., foramen for the internal carotid artery; F.O-NAS., foramen orbitonasale; F.OP., foramen opticum (+ foramen oculomotorius); F.PRO., foramen prooticum; L.OR., lamina orbitonasalis; M.C., lower jaw; OCC.C., occipital condyle; OPERC., operculum; O.PR., otic process; OT.L., otic ledge; PA.QU., pars quadrata; P.E.PL., pars externa plectri; PL.TERM., planum terminale; PR.M.A., processus maxillaris anterior; 'PS'.PR., "pseudobasal" process; SO.NAS., solum nasi; T.NAS., tectum nasi.

The palatoquadrate and its processes

The palatoquadrate has greatly changed its shape and has become reduced to a laterally-compressed cartilaginous plate, roughly triangular in side-view. The pars articularis has rotated farther backwards and lies laterally to the posterior portion of the otic capsule and more or less in the same horizontal plane as the processus "pseudobasalis".

Medially the pars articularis is invested by the lateral wing of the pterygoid bone, posteriorly by the squamosal and laterally by the quadratojugal. The quadratojugal in this region is continuous with a perichondral and endochondral ossification of the postero-lateral portion of the quadrate cartilage. It is impos-

sible to decide from the available material whether this ossification represents a true quadrate or whether it is merely an invasion of the quadrate cartilage by the quadratojugal as is the case in the majority of the *Anura*.

The adult crista parotica has greatly increased in size, not only in a lateral direction but also rostrally. As a result of its great lateral extension the dorsal end of the pars quadrata has been displaced sideways so that the pars quadrata now forms an obtuse angle of approximately 135—140 degrees with the horizontal processus "pseudobasalis" (Fig. 35). The cartilaginous otic connexion between the dorsal end of the pars quadrata and the antero-ventral surface of the crista parotica is situated well in front of the fenestra ovalis and dorso-laterally to the processus "pseudobasalis" (Fig. 35). The "pseudobasal" process, invested ventrally by the medial subotic wing of the pterygoid bone, is more or less club-shaped in ventral view (Fig. 40). It articulates with the ventral and antero-ventral surfaces of the otic ledge in front of the fenestra ovalis (see otic capsule) (Fig. 35). In stage 6 it still articulates with the antero-ventral face of the otic capsule in front of the developing otic ledge. It can, therefore, be reasonably assumed that, with the backward movement and rotation of the pars quadrata, it has been pushed back onto the ventral surface of the otic ledge. At no stage of its development does the adult "pseudobasal" process fuse with the floor of the otic capsule as in *Rana* (Pusey, 1938) and *Bufo* (Ramaswami, 1937). As a result of the backward rotation of the pars quadrata, the front portion of the "pseudobasal" process is now visible in lateral view immediately above the union of the pars quadrata with the processus pterygoideus. As in stage 6 its antero-medial end lies laterally to the prootic foramen and well in front of the origin of both the palatine and the hyomandibular nerves from the prootic ganglionic mass.

The subocular bar (processus pterygoideus) has greatly incresed in length and has the typical arcuate form as in other *Anura* (Figs. 40 & 41).

The anterior end of the neurocranium and the nasal capsules

The os en ceinture, which had not yet started to ossify in the young adult, is now well ossified. Posteriorly it is U-shaped in cross-section and forms the sidewalls and floor of the brain-case in front of the optic foramen. Anteriorly it invades the solum, septum and tectum nasi and reaches forward to the level of the anterior border of the choana. The olfactory nerve passes laterally through the os en ceinture near the front end of the brain-case, and the foramen is, therefore, enclosed in bone. The posterior part of the cavum principale lies in a large recess in the anterior surface of the os en ceinture, and the foramen orbitonasale, transmitting the median branch of the profundus nerve, opens into this recess from behind. A small part of the dorsal border of the foramen consists of cartilage, the free edge of which forms a small ledge overhanging the entrance to the foramen (Fig. 42).

The inferior prenasal cartilage is an antero-ventrally directed curved rod fused

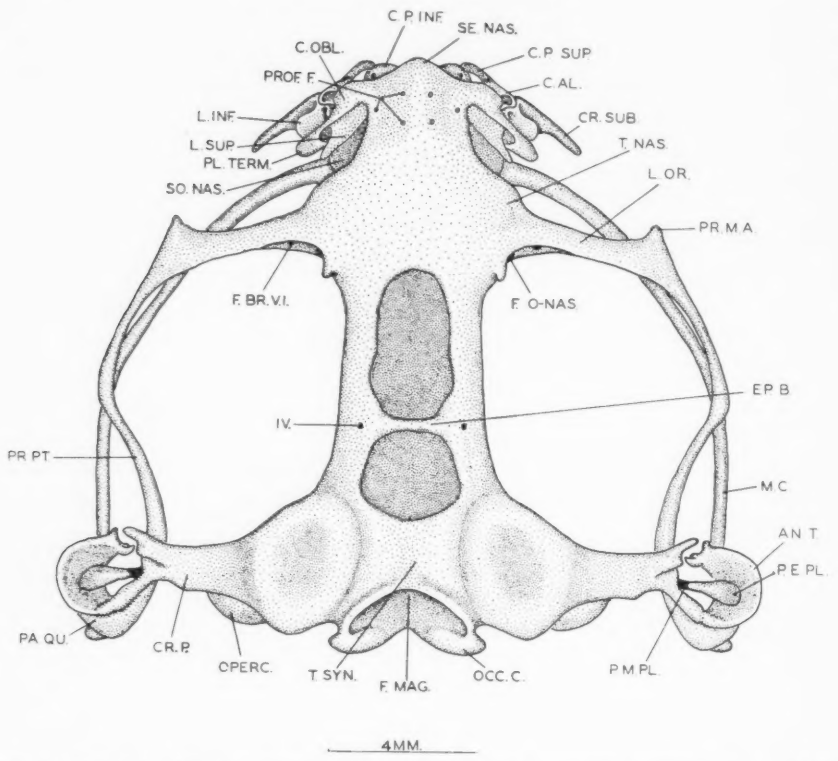

Fig. 41. Stage 7. Graphic reconstruction of the chondrocranium. Dorsal aspect. AN.T., anulus tympanicus; C.AL., cartilago alaris; C.OBL., cartilago obliqua; C.P.INF., cartilago praenasalis inferior; C.P.SUP., cartilago praenasalis superior; CR.P., crista parotica; CR.SUB., crista subnasalis; EP.B., epiphysial bar; F.BR.V.I., foramen for the lateral nasal branch of the profundal nerve; F.O-NAS., foramen orbitonasale; F.MAG., foramen magnum; L.INF., lamina inferior; L.OR., lamina orbitonasalis; L.SUP., lamina superior; M.C., lower jaw; OCC.C., occipital condyle; OPERC., operculum; PA.QU., pars quadrata; P.E.PL., pars externa plectri; PL.TERM., planum terminale; P.M.PL., pars media plectri; PR.M.A., processus maxillaris anterior; PROF.F., foramina for the branches of the profundal nerve; PR.PT., pterygoid process; SE.NAS., septum nasi; SO.NAS., solum nasi; T.NAS., tectum nasi; T.SYN., tectum synoticum; IV., trochlear foramen.

with the solum nasi behind the foramen apicale (Fig. 40). The superior prenasal cartilage, on the other hand, is relatively small and fused with the antero-ventral portion of the cartilago alaris; it supports the facial portion of the premaxillary (Fig. 41). The cartilago alaris forms the lateral cartilaginous support of the entire apertura externa as in *Crinia* (DU TOIT, 1934). Close to its origin from the dorsal surface of the solum nasi the crista intermedia divides into a lamina superior and a lamina inferior. The latter fuses with the planum terminale of the cartilago obliqua, whereas the lamina superior ends freely behind. A well developed crista subnasalis is present (Figs. 40 & 41).

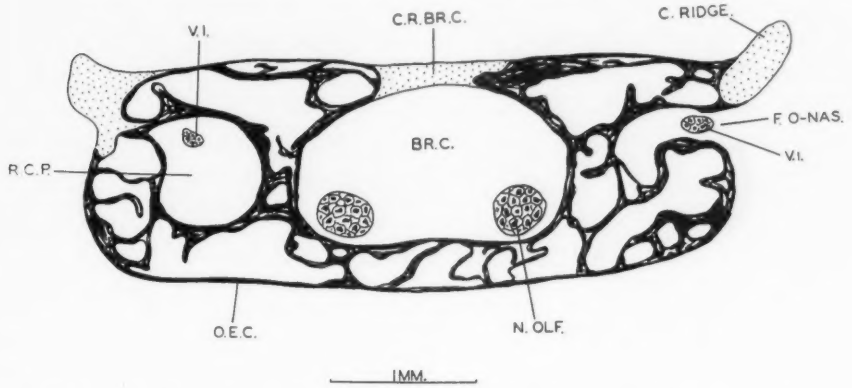

Fig. 42. Stage 7. Transverse section through the os en ceinture in the region of the foramen orbitonasale. BR.C., brain-case; C.R.BR.C., cartilaginous portion of the roof of the anterior portion of the brain-case; C.RIDGE., cartilaginous ridge forming dorsal border of the foramen orbitonasale; F.O-NAS., foramen orbitonasale; N.OLF., olfactory nerve; O.E.C., os en ceinture; R.C.P., recess for the cavum principale; V.1., median nasal branch of the profundal nerve.

The lower jaw

The lower jaw is very similar to that of *Rana* (GAUPP, 1892) and other frogs. A mentomandibular is present. The articular surface of the lower jaw is situated far backward, laterally to the posterior end of the otic capsule (Fig. 40).

The Eustachian tube

The tympanic cavity which has expanded considerably, is connected to the pharynx by the short and wide proximal portion of the original Eustachian tube.

Summary of the Development of the Chondrocranium

The floor of the neurocranium

The premetamorphic stage has a well-developed basal and intertrabecular plate and the former fenestra hypophyseos is already invaded by a single layer of cartilage cells. The usual foramina for the carotid artery and its palatine branch are present. The anterior end of the cranial notochord is embedded in the basal plate, whereas its posterior portion lies in a mid-dorsal groove where a hypochordal bridge is present. During the ontogeny the cranial portion of the notochord becomes reduced, and it disappears by the time the adult stage is reached. At metamorphosis that portion of the floor which lies laterally to the parasphenoid undergoes perichondral erosion along its ventral aspect. The trabecular bridge between the foramina for the internal carotid artery and the ophthalmic artery

is eroded away so that in the adult frog the internal carotid artery enters the brain-case through the side-wall. As a result of the erosion of the cartilage in this region the optic foramen and the craniopalatine foramen come to lie closer to each other, and towards the end of metamorphosis they are confluent. In the adult the exoccipital and prootic bones have encroached on the postero-lateral and antero-lateral portions of the basal plate. The os en ceinture forms the pre-optic portion of the floor of the brain-case.

The side-wall of the neurocranium

In the premetamorphic stage the cartilaginous side-wall has reached its maximum degree of development. Near its anterior end it is pierced by the olfactory foramen. The optic foramen is separated from the oculomotor foramen behind it by the pila metoptica. The trochlear foramen lies above the optic foramen in the dorsal part of the orbital cartilage. A cartilaginous bridge, reminiscent of the supratrabecular bar (DE BEER, 1937) of higher forms, connects the pila antotica with the pila metoptica thus separating the oculomotor foramen from the foramen for the ophthalmic artery above it. The pila antotica forms the anterior border of the large prootic foramen. A small ventrolaterally directed rod of cartilage attached to the dorsal end of the pila antotica, has been identified above as the dorsal vestige of the processus ascendens.

During metamorphosis the foramen opticum becomes very much enlarged by the perichondral destruction along its margins. In this process the optic and oculomotor foramina become confluent by the destruction of the pila metoptica. The lateral surface of the pila antotica also undergoes perichondral erosion thereby destroying the dorsal vestige of the processus ascendens. The trabecular cartilage between the ophthalmic foramen and the primary internal carotid foramen is destroyed so that in the adult the internal carotid artery enters the brain-case through the side-wall.

In the adult the side-wall of the neurocranium in front of the optic foramen is formed by the os en ceinture; the laterally situated olfactory foramen is thus enclosed in bone.

The otic capsule

In the youngest specimen the otic capsule is already completely chondrified and fused with the basal plate. A tectum synoticum, into which may be incorporated a tectum posterius, connects the otic capsules dorsally. The cartilaginous medial wall is pierced by two acoustic foramina as in the majority of the *Anura*. A foramen endolymphaticum, a f. perilymphaticum inferius and a f. perilymphaticum superius are present. Only a thin membrane covers the vertically situated fenestra ovalis.

A larval parotic crest for the attachment of the larval otic process is present in the youngest stage. It is situated on the outer surface of the wall of the lateral

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semicircular canal dorsally to the posterior portion of the fenestra ovalis. During metamorphosis it is destroyed and the adult parotic crest develops on the wall of the lateral semicircular canal dorsally to the anterior part of the fenestra ovalis. Its proximal part appears to develop as an outgrowth of the wall of the lateral semicircular canal, whereas its distal portion seems to rechondrify in the mass of cartilage cells liberated by the erosion and disintegration of the larval otic process and the posterior portion of the palatoquadrate. Subsequently this new cartilage fuses with the median capsular part of the parotic crest, and its antero-ventral part grows downward to merge into the dorsal end of the now vertically situated pars quadrata, thus forming the otic process of the adult. In older adults the crista parotica has grown into a ledge of considerable size with which the posterior arm of the anulus tympanicus is confluent.

The ventral rim of the fenestra ovalis (lateral border of the capsular floor in this region) grows out in a lateral direction during late metamorphosis to form a cartilaginous ledge which forms the floor of the fossa fenestrae ovalis. Its dorsally directed lateral edge, the crista praeopercularis, fuses with the ventral border of the pars interna plectri. In the adult the ossification of the pars interna plectri has invaded the crista praeopercularis. A large ductus fenestrae vestibuli is present in postmetamorphic stages.

Another interesting feature of the otic capsule is the development of an otic ledge. During metamorphosis a narrow strip of juvenile cartilage develops on the antero-lateral surface of the side-wall of the otic capsule. Although the evidence is not conclusive, it would appear that like the otic process, this strip of cartilage is derived from the cells liberated by the disintegration of the larval otic process and the posterior part of the palatoquadrate. This cartilaginous strip stretches from the base of the adult crista parotica to the antero-ventral rim of the fenestra ovalis where it fuses with the anterior end of the crista praeopercularis. In this region a block of cartilage, the otic ledge, develops on the side-wall of the otic capsule. It is not improbable that some of the aforementioned cells contribute towards the formation of the otic ledge. The first cartilage bone to appear in the chondrocranium is the exoccipital. It starts to develop in the occipital arches, but soon spreads to the posterior portion of the otic capsule and the posterolateral part of the tectum synoticum and of the basal plate. The exoccipital is soon followed by the prootic bone which ossifies in the anterior wall of the capsule. Like the exoccipital, it soon spreads to the tectum synoticum and to the basal plate. In the adult the exoccipital and prootic are fused, and the ossification invades the proximal half of the parotic crest so that the adult otic capsule is almost completely composed of bone.

The fenestra ovalis and the sound-conducting apparatus

In the youngest stage a very thin membrane covers the fenestra ovalis. Mesenchymatous cells, originating from the ventral lip of the fenestra ovalis, migrate

onto the lateral surface of this membrane. The chondrification of the operculum sets in in the posterior half of the membrane about equidistant from the dorsal and ventral rims of the fenestra. From here it spreads in all directions, becoming saucer-shaped in cross-section, until it occludes the posterior half of the fenestra ovalis. Its posterior end soon grows back beyond the posterior rim of the fenestra ovalis where it fuses with the side-wall of the otic capsule. Fusion also occurs between the postero-dorsal rim of the fenestra ovalis and the operculum. The musculus opercularis becomes inserted on the lateral surface of the operculum and not on a special tuberosity as in many other forms.

Chondrification of the pars interna plectri starts in the anterior portion of the membrana fenestrae ovalis. Its posterior end soon comes to occupy a position mesially to the antero-dorsal end of the operculum, whereas its anterior end develops a laterally-directed process, the pars media plectri. The latter chondrifies in a mesenchymatous strand that stretches from the anterior end of the pars interna plectri in an antero-lateral direction to the laterally situated mesenchymatous disk, the anlage of the pars externa plectri and of the anulus tympanicus. In the adult the pars media plectri and the greater part of the pars interna plectri become ossified. The cartilaginous pars externa plectri is connected to the latero-ventral surface of the crista parotica by a cartilaginous bar, the processus ascendens partis externae plectri. The sickle-shaped anulus tympanicus starts to chondrify slightly earlier than the pars externa in the same mesenchymatous disk. The posterior arm of the anulus is fused with the parotic crest and the discontinuity faces antero-dorsally.

The roof of the neurocranium

The tectum synoticum, with which may be fused a tectum posterius, connects the otic capsules dorsally. It consists of cartilage in the youngest larva, but during metamorphosis it is invaded by the exoccipital and prootic bones, so that in the adult only its narrow mid-dorsal portion remains cartilaginous.

The orbital cartilages are united dorsally by a cartilaginous rod, the epiphyseal bar. It is already present in the youngest larva and persists into the adult without undergoing any fundamental change.

The cartilage forming the roof of the anterior end of the brain-case is not invaded by the os en ceinture.

The palatoquadrate and its processes

In the younger stages the palatoquadrate is a flat elongate plate of cartilage lying laterally to, and more or less parallel with, the cranial floor. The commissura quadrato-cranialis anterior is broad, and the subocular vacuity is small. A small quadrato-ethmoidal process is present on the anterior edge of the quadrato-cranial commissure. A "pseudobasal" process connects the palatoquadrate with the anterior part of the floor of the otic capsule (and with the basal

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plate?). The otic process anchors the posterior end of the palatoquadrate to the larval parotic crest dorsally to the posterior half of the fenestra ovalis. A small cartilaginous rod on the outer surface of the pila antotica is the dorsal vestige of the ascending process. In addition to the cartilaginous connexions, three ligaments connect the palatoquadrate to the neurocranium. These are the ligamentum cornu-quadratum mediale between the processus quadrato-ethmoidalis and the ventral flange of the ethmoidal plate, the ligamentum cornu-quadratum laterale between the antero-lateral tip of the palatoquadrate and the antero-lateral border of the ethmoidal plate, and the quadrato-otic ligament connecting the hind end of the palatoquadrate to the floor of the hind end of the otic capsule.

The dorsal vestige of the ascending process, present in the younger stages, soon disappears from the lateral surface of the pila antotica.

The larval otic connexion is severed by the erosion and eventual disintegration of the larval otic process. The cartilage cells thus liberated condense into an irregular mass on the lateral surface of the otic capsule. The fate of these cells has already been dealt with (see otic capsule).

The larval "pseudobasal" process is the second to be destroyed. Its destruction is preceded by a general "softening" of its cartilage. The cartilage cells liberated by its destruction rechondrify as the adult "pseudobasal" process which later fuses with the medial surface of the pars quadrata.

The destruction of the connexion of the commissura quadrato-cranialis anterior to the neurocranium proceeds as follows: the perichondral erosion which starts along its caudal border is so complete proximally that its connexion with the neurocranium is severed. Only its lower front portion with the processus quadrato-ethmoidalis remains intact. The latter now lies mesially to the posterior tip of the developing processus maxillaris posterior with which it soon fuses to form the processus pterygoideus. This process, therefore, has a double origin.

Meanwhile, that portion of the larval palatoquadrate behind the ceratohyal notch has been destroyed, and the remaining anterior portion of the palatoquadrate, the pars quadrata, has started its backward rotation. By the time the adult stage is reached it has rotated through an angle of approximately 135—140 degrees. There is no buckling and folding of the posterior portion of the palatoquadrate during metamorphosis as in *Rana* and *Bufo*.

The lower jaw

The larval lower jaw structures are the two medio-ventrally situated infrarostrals, and the latero-ventrally situated paired Meckel's cartilages. Each cartilage of Meckel is a heavily built structure attached by a commissura intramandibularis to the antero-lateral face of the infrarostral of its side.

During metamorphosis the lower jaw cartilages undergo perichondral erosion and become round in cross-section. The infrarostral fuses with Meckel's cartilage of its side, and the combined structure thus formed increases in length to form

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the lower jaw of the adult. The articular surface of Meckel's cartilage which, in the larva, faces downwards soon faces upwards. In the adult it lies opposite the hind end of the otic capsule. A weakly developed mentomandibular is present in the old adult.

The anterior end of the chondrocranium and the suprarostral apparatus

The antero-lateral projections of the ethmoidal plate in the youngest stage probably represent the trabecular horns. Attached to each trabecular portion of the ethmoidal plate there is a ventrally-directed flange which articulates with the lateral surface of the median portion of the suprarostral cartilage. A tunnel is thus formed between the dorsal ethmoidal plate and the ventrally situated median portion of the suprarostral cartilage. In the posterior part of this tunnel lies the anterior end of the preoral buccal cavity. Dorsally to the lateral wing of the suprarostral cartilage lies an independent triangular cartilage, the dorsal rostral. The olfactory nerve pierces the side-wall of the brain-case near its anterior end. A narrow tectum nasi is already present in front of the lamina orbitonasalis.

The destruction of the cartilages in this region starts, during metamorphosis, in the dorsal rostrals, then proceeds to the antero-lateral portion of the ethmoidal plate, the lateral wings of the suprarostral cartilage and finally to the median portion of the latter. Meanwhile, the constituent parts of the nasal capsules have started to chondrify. The nasal capsule of the adult does not differ much from that of other forms. The os en ceinture invades the solum, the tectum and the septum nasi, and in the old adult reaches forward to the anterior level of the choana. A large recess in the anterior face of the os en ceinture houses the posterior part of the cavum principale.

Discussion

The *Amphibia* are undoubtedly derived from the Crossopterygii, but there is still no general agreement about their origin and the course of their early evolution. According to the older and generally accepted view they are a monophyletic group, which, early in the course of their evolutionary history, differentiated into several lines of development. One of these led to the reptiles, some became extinct while others culminated in the living orders. A more recent view developed particularly by the Swedish school of palaeontologists, and which is slowly gaining acceptance, is that they are at least diphyletic in origin. Whichever view is accepted it must be emphasized that the recent *Amphibia* are highly specialized end-products of evolution. The interpretation of results of work on recent *Amphibia* should always be considered against this background, and due care should be exercised in attempting to establish homologies.

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The Chondrocranium of Heleophryne Purcelli Sclater

A. THE PALATOQUADRATE AND ITS PROCESSES

The palatoquadrate of the anuran larva may be suspended from the neurocranium by four cartilaginous processes. These are, from in front backwards, the commissura quadrato-cranialis anterior, the processus ascendens, the processus "pseudobasalis" and the processus oticus. If it is accepted that the "pseudobasal" process is not homologous with the basal process of *Urodela* and *Apoda,* we are faced with the problem of five possible dorsal attachments of the mandibular arch in the *Amphibia.*

It is a well-established fact that the mandibular and hyoid arches are serially homologous with the branchial arches. In *Eusthenopteron* JARVIK (1954) has shown that the dorsal ends of the first and second branchial arches are bifurcated and following VAN WIJHE (1882), he calls the two prongs the infrapharyngobranchial and the suprapharyngobranchial. Somewhat similar conditions obtain in several recent fishes. For further details regarding the dorsal parts of their branchial arches the reader is referred to the works of DE BEER (1937) and JARVIK (1954) both of whom review the literature on this subject. The results of paleontological, comparative anatomical, and embryological studies by various authors strongly suggest that the hyomandibular and the palatoquadrate are the epihyal and epimandibular respectively. Moreover, recent studies particularly by HOLMGREN (1940, 1943) and JARVIK (1954) show that parts of the premandibular arch are in all probability incorporated into the palatoquadrate. If the larval palatoquadrate of the *Anura* is a simple epimandibular one would except it to have only two dorsal attachments. But this is not the case. The larger number of viscero-neurocranial connexions could reasonably be explained by assuming that the larval as well as the adult palatoquadrate of *Anura,* and other living *Amphibia,* for that matter, is a compound structure incorporating certain elements of the presumed premandibular arch in front, and of the hyoid arch behind it; the latter, in any case, lacks some of the elements of the post-otic visceral arches.

The commissura quadrato-cranialis anterior and the pr. pterygoideus

In *Heleophryne,* as in other *Anura,* the commissura quadrato-cranialis anterior is partly destroyed during metamorphosis. Its antero-ventral portion, with its quadrato-ethmoidal process, and the processus maxillaris posterior of the lamina orbitonasalis form the processus pterygoideus of the adult. As in *Ascaphus* (VAN EEDEN, 1951), the processus maxillaris posterior may, perhaps, chondrify independently of the lamina orbitonasalis, but whether it is derived from the quadrato-cranial commissure, as in *Calyptocephalus* (REINBACH, 1939), and possibly also in *Ascaphus* (VAN EEDEN, 1951), was impossible to establish, since intermediate stages were not available. However, the fact that this process may chondrify independently seems to suggest that it does not necessarily belong to the orbitonasal lamina. More or less the same condition obtains in *Salamandra atra,*

Ambystoma punctatum, Spelerpes bilineatus (WIEDERSHEIM, 1877; EDGEWORTH, 1923), *Salamandra maculosa* (STATDMÜLLER, 1924), *Ictalurus* (RYDER, 1877), *Amiurus* (KINDRED, 1919; WELLS, 1922) and *Clupea* (WELLS, 1922); in these the processus pterygoideus chondrifies independently of the palatoquadrate. According to FOX (1954, p. 259) its development in *Cryptobranchus japonicus* "suggests that the processus pterygoideus is at least in part probably formed as an independent chondrification *in situ*". It therefore seems reasonable to assume that the processus pterygoideus is not primarily part of the mandibular arch, and it is suggested that it belongs to the premandibular arch, part of which has become incorporated into the palatoquadrate during phylogeny. This is in accordance with the views held by JAEKEL (1899, 1925, 1927) and JARVIK (1954) who regard the pars autopalatina as belonging to the premandibular arch.

The processus basalis and the processus "pseudobasalis"

GEGENBAUER (1872) regarded the otic process as the morphological dorsal end of the mandibular arch. HUXLEY (1876), on the other hand, maintained that the basal process is the dorsal end, and his views are now generally accepted. The basal process may therefore represent either the ventral proximal articular head of the epimandibular or the infrapharyngomandibular.

It is generally agreed that the process of the palatoquadrate which establishes the basal articulation with the basipterygoid process in tetrapods, other than the *Anura,* is a true basal process. DE BEER (1926) was the first to focus attention on the different relationship of the palatine nerve to this process in the *Anura,* and he introduced the term "pseudobasal connexion". KRUIJTZER (1931), although retaining the old terminology, claimed that the process in *Megalophrys* (*Megophrys*) is of hyoid origin. PUSEY (1938) rejected the homology of the basal process with the process in the *Anura* for which he suggested the term "pseudobasal process".

It is difficult to believe that another process with the same relations to the palatoquadrate and with the same function has been substituted for the basal process in the *Anura.* The circumstance that the "pseudobasal" process chondrifies independently of the palatoquadrate and establishes a postpalatine articulation is not enough evidence to believe that such an exchange has indeed taken place. According to SEWERTZOFF and DISLER (1924) the basal process in *Laemargus* arises separately and represents the pharyngomandibular. DE BEER (1926, p. 336) in discussing the basal process states: "In embryonic stages of *Mustelus, Scylliorhinus,* and *Squalus* it arises separately and later fuses onto the pterygoquadrate median to the orbital process". HOLMGREN (1943) is of opinion that the separate anlage in the above-mentioned genera is in reality a suprapharyngomandibular, which, as will be pointed out later, cannot be homologized with the basal process. The only real objection to the proposed homology of the basal process with the "pseudobasal" process, therefore, seems to be their relationship to the palatine nerve. This aspect of the problem will be discussed below.

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Although a "pseudobasal" connexion is present in the larva of *Heleophryne, Ascaphus* (VAN EEDEN, 1951), *Rana curtipes* (RAMASWAMI, 1940) and in *R. afghana* (RAMASWAMI,1943), it only develops during meamorphosis in the other *Anura* hitherto investigated. In the youngest larva of *Heleophryne* used for the present investigation it is already present, forming a cartilaginous bridge between the floor of the otic capsule and the palatoquadrate. It lies behind the palatine nerve whereas the hyomandibular nerve and the lateral head vein pass backward dorsally to it. Nothing is known about its early development in *Heleophryne* or in any other anuran where it occurs in the larval form.

The adult palatobasal connexion, and especially its lateral portion, the "pseudobasal" process, is formed by the rechondrification of the tissue liberated when the larval "pseudobasal" connexion is destroyed during early metamorphosis. The adult "pseudobasal" process thus arises as an independent structure, but soon fuses with the mesial surface of the palatoquadrate.

Although GAUPP (1893) regarded the "pseudobasal" process in *Rana* as a true basal process, he was puzzled by its mode of development. According to PUSEY (1938, p. 530) the "pseudobasal" process of *Rana* and other *Anura* develops partly out of the otic capsule and partly as a condensation in situ and it "represents the outer end of the basitrabecular process from the basal plate which has separated off from the cranial floor by the destruction of its root. It is suggested that it has become fused secondarily to the quadrate . . ." KRUIJTZER (1931) describes its independent origin in *Megalophrys montana* and *Alytes* and claims that it is homologous with the pharyngohyal of *Neoceratodus*. In *Leiopelma* (E. M. STEPHENSON, 1951) a "pseudobasal articulation" is present in the adult. Since the orbital artery pierces the chondrifying "pseudobasal" connexion in young posthatching stages N. G. STEPHENSON (1951) claims that it is of hyoid origin and proposes the terms otohyoid ledge and hyobasal process for the otic ledge and "pseudobasal" process respectively. In *Bufo* (RAMASWAMI, 1936; SEDRA, 1950; BARRY, 1956) these structures are fused in the adult, thus forming a "pseudobasal connexion". SEDRA (1950) claims that "pseudobasal" connexion in *Bufo regularis* has a double origin. Its proximal part, representing the otic ledge, which he mistakenly calls the pseudobasal process, grows out from the otic capsule. Its extreme distal part, the "pseudobasal" process, rechondrifies in the cells liberated by the destruction of the posterior end of the palatoquadrate. These two anlagen soon fuse. BARRY (1956) describes a similar double origin for the "pseudobasal" connexion of *Bufo angusticeps*. It would, therefore, appear that in all the *Anura* hitherto investigated, the component parts of the "pseudobasal" connexion arise in fundamentally the same way.

From the above it may be concluded that the "pseudobasal" process is homologous in all *Anura*, but its homology within the vertebrate group needs further investigation. Gaupp's view that it is a true basal process was generally accepted until DE BEER (1926) drew attention to the fact that the basal articulation is

effected behind the palatine nerve. De Beer (1926, p. 336) himself did not doubt the homology of the basal process as he states that "the basal process is well developed, but instead of fusing with the basitrabecular process it fuses with the post-palatine commissure". Subsequent workers began to doubt its homologies with a true basal process, and regarded it as a "pharyngohyal" Kruijtzer, 1931), "the outer end of the basitrabecular process" (Pusey, 1938), a hyobasal process (N. G. Stephenson, 1951) and the homologue of the processus paratemporalis of *Eusthenopteron* (Jarvik, 1954).

Typically, the palatine nerve passes down by the side of the parachordal, behind the basipterygoid process and then proceeds forwards beneath it. It is clear that the palatine nerve, although morphologically behind the basal process, does not pass down immediately behind it, but medially to it. It is, therefore, suggested that the "pseudobasal" process of *Anura* is homologous with the basal process of other tetrapods and that in the course of phylogeny it has slipped back off the basipterygoid process onto the ventral surface of the otic ledge, thus giving rise to a postpalatine articulation. The palatine nerve was in no way associated with this backward movement of the basal process since it passed down medially to the latter. With the disappearance of the basipterygoid process the condition in adult *Anura* was established. It is, therefore, suggested that the use of the term "pseudobasal process" should be discontinued. In any case, the prefix"pseudo-" in anatomical nomenclature should be discouraged, as a structure is a unit sui generis not a false type of something else.

What, then, is the nature of the basal articulation in the *Anura*? This problem can hardly be discussed without first establishing the morphological significance of the basal process.

According to Huxley's view, which is generally accepted, the basal process represents the morphological dorsal end of the mandibular arch. Our first problem is, therefore, to determine the homology of the anatomical dorsal end of the mandibular arch. A convincing case can be made out for homologizing the pars quadrata with an epimandibular. The evidence for this conclusion derives from comparative anatomical, embryological and palaeontological sources. The comparative anatomical evidence is based on its relationships to neighbouring skeletal parts, muscles, bloodvessels and nerves. Structures, mainly of a transitory nature, identified as pharyngomandibulars and hypomandibulars in the ontogeny of certain forms, provide the embryological evidence for homologizing the pars quadrata with an epimandibular. The palaeontological evidence is restricted to the relationship of the pars quadrata to neighbouring skeletal parts, but is strengthened by Jarvik's critical analysis of the mandibular and other visceral arches of *Eusthenopteron*. Since it has been proved that the pharyngeal portion of a typical visceral arch, such as the first or the second branchial arch, primitively consists of an infrapharyngeal and a suprapharyngeal element, it follows that the dorsal end of an epimandibular must have a ventral and a dorsal arti-

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cular head. If we assume that the pars quadrata of the *Anura* is the epimandibular we must next decide whether the processus basalis represents its dorsal or its ventral articular head. It is also possible that the processus basalis belongs to the pharyngomandibular, in which case we must decide whether it is an infrapharyngomandibular or a suprapharyngomandibular.

The processus basalis, like the infrapharyngomandibular, is always ventral to the vena capitis lateralis, but, as the suprapharyngomandibular is dorsal to this vein, it cannot be considered as the homologue of the processus basalis. The same evidence seems to exclude the dorsal articular head of the epimandibular as representing the basal process.

If the evidence has been interpreted correctly, the homologue of the processus basalis must be sought either in the ventral articular head of the epimandibular or in the infrapharyngomandibular. SEWERTZOFF and DISLER (1924) regard it as a pharyngomandibular. The concept of the bifurcated nature of the pharyngal elements, first enunciated by VAN WIJHE (1882) had not yet gained general acceptance in 1924, and consequently, Sewertzoff and Disler did not distinguish between infrapharyngomandibular and suprapharyngomandibular. In the light of modern knowledge we can safely conclude that they were referring to an infrapharyngomandibular.

JARVIK (1954) regards the basal process as the ventral articular head of the epimandibular, and the suborbital ledge and the basipterygoid process of *Eusthenopteron* as representing the infrapharyngomandibular. However, JARVIK (1954, p. 75, footnote) states that "whether a structure strictly homologous with the process in *Eusthenopteron* called the basipterygoid process in this paper ever has been established in recent lower vertebrates seems doubtful".

According to CROMPTON (1953) and FRANK (1954) the basipterygoid process of *Spheniscus* and *Struthio* arises autochthonously and then chondrifies in continuity with the neurocranium. ENGELBRECHT (1958, p. 175) is more to the point when he states that "the pr. basipterygoideus of *Pyromelana* chondrifies in the dorsal portion of the quadratopolar commissure, it is of visceral origin, and its connexion to the nerucranium is secondary". The quadratopolar commissure develops as an outgrowth of the pars quadrata which then fuses with the anteroventral corner of the polar cartilage. For this reason FILATOFF (1906, quoted from ENGELBRECHT, 1958) regards it as a continuation of the pars quadrata.

The proc. basipterygoideus, therefore, seems to belong to the mandibular arch. If this is so, it must represent the infrapharyngomandibular, and the basal process must belong to the epimandibular. It is therefore concluded that the basipterygoid process and the basal process represent the infrapharyngomandibular and the ventral articular head of the epimandibular respectively. The infrapharyngomandibular, as represented by the basipterygoid process, is absent in the *Anura* unless it is represented by the larval suborbital ledge which is destroyed during metamorphosis.

In all *Anura* the basal process has established a postpalatine articulation or synchondrosis, as the case may be, with another process, the otic ledge, which appears to be serially homologous with the basipterygoid process. It lies behind the palatine nerve, and the lateral head vein and the hyomandibular nerve pass backwards dorsally to it. Moreover, it lies morphologically dorsal to the internal carotid artery. Its relations to the nerves and bloodvessels of this region are the same as those of an infrapharyngohyal. But the same applies to the proximal portion of the plectrum (and operculum), and both structures cannot represent separate infrapharyngohyals. It will be argued below (see sound-conducting apparatus) that all these structures are derivatives of the original infrapharyngohyal.

If the otic ledge represents the infrapharyngohyal (or a portion of it) which has become incorporated into the otic capsule, and if the basal process represents the proximal articular head of the epimandibular, we have in the skull of adult *Anura* an articulation between the epimandibular and the infrapharyngohyal. This is in accordance with the condition in *Amia* where Allis (1897) found interarcual articulations between the infrapharyngobranchial of one arch and the epibranchial of the preceding one. In *Amia,* however, the epibranchial has two distinct anterior articular heads, a terminal one articulating with the infrapharyngobranchial of the same arch, and a medial one forming the interarcual articulation. Should future investigations show that the so-called "pseudobasal" process of *Anura* is serially homologous with the anterior medial articular head of an epibranchial of *Amia,* then it cannot be a true basal process. In that case it may prove to be the equivalent of the paratemporal process of *Eusthenopteron* as suggested by Jarvik (1954). Jarvik (1954) also regards the otic ledge (otic shelf) as the infrapharyngohyal. The cartilaginous connexion which, in *Heleophryne,* develops during metamorphosis between the otic ledge and the parotic crest may be something similar (not homologous) to the commissura terminalis which connects the ceratobranchials of *Anura* and of certain *Urodela* dorsally. In *Probeviceps* (author) this cartilaginous connexion is extremely well-developed so that the parotic crest and the otic ledge form a continuous block of cartilage in front of the fenestra ovalis, the lateral head vein and the hyomandibular nerve passing backwards in a longitudinal groove along its lateral surface.

If the assumption that the infrapharyngohyal has become incorporated into the ventro-lateral wall of the otic capsule is correct, then the fact that the otic ledge in some forms, e.g. *Bufo* (Sedra, 1950; Barry, 1956), develops from the base of the otic capsule is easily explained.

It is, therefore, concluded that the otic ledge is a derivative of the infrapharyngohyal and that the basal process is the ventral articular head of the epimandibular. The articulation between them is, therefore, interarcual and de Beer's term "pseudobasal articulation" could be retained for this type to distinguish it from the intra-arcual articulation of other forms.

Kruijtzer (1931), apparently on the strength of topographical relationships

only, maintains that the basal process is a derivitive of the pharyngohyal. N. G. STEPHENSON (1951), while rejecting this homology, nevertheless claims a hyoid origin for the basal process. E. M. STEPHENSON (1951) (and by implication also N. G. Stephenson) claims that the combined otohyoid ledge and hyobasal process of *Leiopelma* are homologous with the hyomandibular of fishes. Her main reasons for doing so seem to be the fact that the procartilaginous palatobasal connexion of *Leiopelma* is pierced by the orbital (stapedial) artery, that it chondrifies independently of the palatoquadrate and that its procartilaginous anlage is connected by a distinct mesenchymatous tract of cells to the ceratohyal below it. This view seems to be unacceptable since HOLMGREN (1940, 1943) has shown that the orbital artery does not pierce the hyomandibular, but the otic shelf (otic ledge) which chondrifies independently, and which is connected by a ligament to the lower end of the hyomandibular.

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The processus ascendens

In the youngest larvae of *Heleophryne* used for the present investigation a small cartilaginous rod is attached to the dorsal end of the pila antotica. Since it bears all the relations to the branches of the trigeminal nerve as does a true ascending process it is identified as a dorsal vestige of the latter. As younger stages were not available its early development is unknown. It may be either the only portion of the ascending process to develop or it may be a vestige of an ascending process which breaks down early in the ontogeny.

RAMASWAMI (1938) did not find an ascending process in the tadpoles of *Philautus variabilis* but noted that earlier stages were not available for study. It is, however, present in all other anuran tadpoles hitherto studied. It breaks down during ontogeny and is absent in the adult. A notable exception is *Ascaphus* in which VAN EEDEN (1951) found an ossified dorsal vestige (alisphenoid) of this process.

As the processus ascendens forms a bridge outside the jugular vein JARVIK (1954) regards it as a suprapharyngomandibular. If this is correct we may conclude that both the suprapharyngomandibular (ascending process) and the infrapharyngomandibular (basipterygoid process) are absent in the adult anuran skull.

The otic process

The homologies of the otic process are by no means certain. GEGENBAUR (1871) was wrong in regarding it as the dorsal end of the mandibular arch. In fact, it is doubtful whether it belongs to the mandibular arch at all. GAUPP (1893) considers the larval otic process as a larval specialization confined to the *Anura* whereas the adult process, of palatoquadrate origin, is the homologue of the otic process of *Urodela*. PARKER (1871) was of the opinion that the upper end of the hyoid arch is fused on to the posterior side of the mandibular arch. He

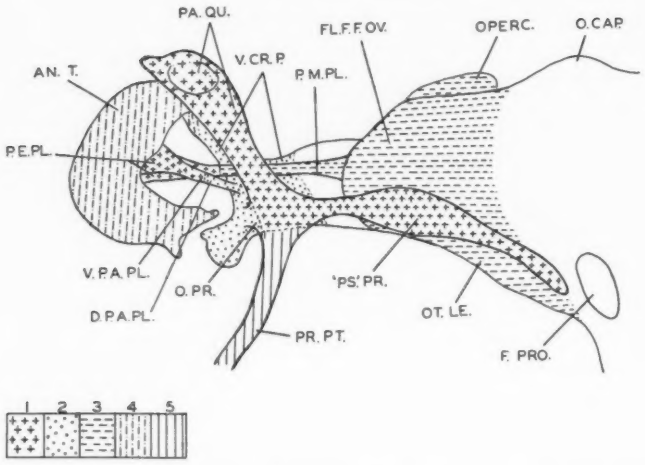

Fig. 43. Diagrammatic representation of the dorsal elements of the mandibular and hyoid arches of the adult. Ventral view. F.PRO., foramen prooticum; O.CAP., otic capsule. 1. epal elements: epimandibular (PA.QU., pars quadrata: 'PS'.PR., basal ("pseudobasal") process); epihyal (P.E.PL., pars externa plectri; V.P.A.PL., ventral portion of the processus ascendens partis externae plectri). 2. suprapharyngohyal (D.P.A.PL., dorsal portion of the processus ascendens partis externae plectri; O.PR., otic process; V.CR.P., lateral (visceral) portion of the crista parotica). 3. infrapharyngohyal (FL.F.F.OV., floor of the fossa fenestra ovalis; OPERC., operculum; OT.LE., otic ledge; P.M.PL., pars media plectri). 4. stylohyal (?) (AN.T., anulus tympanicus). 5. premandibular arch (PR.PT., processus pterygoideus).

regarded the larval otic process ("suprahyomandibular") as the dorsal end of the hyoid arch and the adult process as a derivative of the ascending process. KRUIJTZER (1931) describes a cartilaginous nodule, a "laterohyal", as effecting the cartilaginous connexion between the otic process and the crista parotica in *Megalophrys* (*Megaphrys*) *montana*. According to PUSEY (1938) "the whole outer border of the quadrate bar, from the edge of the auditory capsule to the anterior edge of the muscular process, is to be looked upon as a single very much stretched otic process; the tadpole otic process would then be the original connexion of this process with the auditory capsule".

VAN EEDEN (1951) maintains that the anterior portion of the adult crista parotica (Gaupp's pars cartilaginea, 1896) is of palatoquadrate origin in *Ascaphus* and constitutes the adult otic process. N. G. STEPHENSON (1951), on the other hand, describes the crista parotica as a ridge formed by the backward extension of the otic process in the post-hatching period of development in *Leiopelma*.

In larval *Heleophryne* that portion of the palatoquadrate which lies behind the basal process bears all the relations to the nerves and bloodvessels as does a true otic process, and for this reason I regard it as the homologue of the larval otic process of other *Anura*. It is destroyed during metamorphosis, and the cells

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thus liberated rechondrify on the lateral edge of the parotic crest. This lateral portion of the parotic crest (Gaupp's pars cartilaginea) grows forward and downward to fuse with the dorsal end of the pars quadrata. It therefore follows that in *Heleophryne,* and probably also in *Ascaphus* and other *Anura* where both processes occur in the ontogeny, the larval and adult otic processes are strictly homologous. It is noteworthy that in *Leiopelma* (N. G. Stephenson, 1951), which has a direct development without a tadpole stage, the otic process retains an unbroken connexion with the otic capsule throughout development and that it forms the adult parotic crest.

A larval otic process is not present in the developmental stages of all *Anura.* It is, for instance, absent in *Bufo* (Ramaswami, 1940; Sedra, 1950; Barry, 1956), *Rana curticeps* (Ramaswami, 1940), *Alytes* (Peeters, 1910), *Discoglossus* (Pusey, 1938), and *Polypedates* (Okutomi, 1937). Since it is invariably present in the adults it is suggested that in the larvae it is represented by the posterior (especially the postero-lateral) portion of the larval palatoquadrate of these forms. It is of interest that Sedra (1950) found a "thin fibrous ligament" which connects the postero-lateral edge of the larval palatoquadrate of *Bufo* with the crista parotica.

In his description of the larval otic process of *Rana temporaria,* Pusey (1938, p. 489) describes it as a small rod of cartilage that "is thickest at its hinder end", that is, the end which is fused with the otic capsule. According to Gaupp (1892, p. 435) the chondrification of the otic process "findet übrigens nicht allein im Anschluss an das Qudratum statt, sondern auch von der Ohrkapsel aus schiebt sich ein kurzer stumpfer Knorpelfortsatz in jenes Band hinein vor und verschmilzt mit dem vom Quadratum aus kommenden". The thicker hind portion of Pusey's larval otic process then probably represents the larval parotic crest.

In the youngest stage of *Heleophryne* at my disposal (slightly younger than my stage 1) the medial side of the hind end of the palatoquadrate (otic process of this paper) has started to fuse with the latero-ventral surface of the small, but prominent, larval parotic crest, which is presumably of capsular origin. In stage 1 the fusion is complete and the hind end of the palatoquadrate (otic process) projects backwards beyond the point of fusion. Had the younger stage not been available it would have been tempting to homologize the larval parotic crest with a small otic process similar to the one described for *Rana* by Pusey (1938). Although it remains relatively short in later stages it gives the impression of a small cartilaginous rod that "is thickest at its hind (inner) end". It would be worth while to reinvestigate the early development of the larval otic process of *Anura* to determine what part, if any, is of capsular origin.

The condition in *Ascaphus* (Pusey, 1943; van Eeden, 1951) is reminiscent of that in *Heleophryne.* Here, as in *Heleophryne,* the hind portion of the larval palatoquadrate probably represents the otic process. Unlike that of *Heleophryne* it establishes two connexions with the otic capsule, one behind and one in front

of Pusey's "critical vein". The posterior of these two connexions seems to correspond to the otic connexion of *Heleophryne*.

It has been suggested earlier that the ascending process probably represents the original suprapharyngomandibular. It then follows that the otic process, which has the same relations to the nerves and bloodvessels as a suprapharyngeal element, cannot be the suprapharyngomandibular. What, then, is its true nature? Is it present in some form in the early crossopterygian skull?

ALLIS (1914, p. 635) first advanced the theory that the lateral wall of the trigemino-facialis chamber (lateral commissure of DE BEER, 1926) represents the otic process in *Ceratodus:* "The processus oticus thus being represented, when present, in Amia, teleosts and selachians, in a part of the cranial wall of those fishes . . ." DE BEER (1926, p. 359) critizes Allis's theory along the following lines: "(1) the confusion of cranial and visceral structures; (2) the impossibility of the theory when applied to the Selachii; (3) the true nature of the lateral commissure and pila lateralis as evidenced by their development and the relations of the palatine nerve". It is, however, interesting to note that according to his table on p. 366 a lateral commissure is absent in those forms that possess a definite otic process. In other words, both processes do not occur together although, of course, both may be absent.

If Allis's theory is correct, then the lateral commissure must be a visceral element, whereas DE BEER (1926) maintains that it is a true neurocranial structure. De Beer's criticism would fall away if the ontogeny were to show that the lateral commissure is of visceral origin. It is noteworthy that according to DE BEER (1937, p. 208) the Selachian prespiracular cartilage "appears to represent the entire otic process of the adult". According to HOLMGREN (1940) the prespiracular cartilages chondrify in the same "prespiracular complex" as does the lateral commissure.

In his studies on the development of the skull in sharks and rays HOLMGREN (1940) clearly shows that the lateral commissure develops as a process of the palatoquadrate which becomes detached from the latter and fuses on to the neurocranium to form the side-wall of the trigemino-facialis chamber. Its development follows a similar pattern in *Amia* and teleosts (HOLMGREN, 1943). HOLMGREN (1943) is of the opinion that ALLIS (1914) was right when comparing the lateral commissure with the otic process of *Ceratodus*. Furthermore, he regards the lateral commissure as modified mandibular ray bars. JARVIK (1954) on the other hand regards the lateral commissure of *Eusthenopteron* as a suprapharyngohyal.

It is, therefore, concluded that the otic process is homologous with the lateral commissure as suggested by Allis and that it may represent either modified mandibular ray bars or a suprapharyngohyal. Since the otic process appears to be serially homologous with the processus ascendens, which has been identified as the suprapharyngomandibular, it would appear logical to assume that the otic

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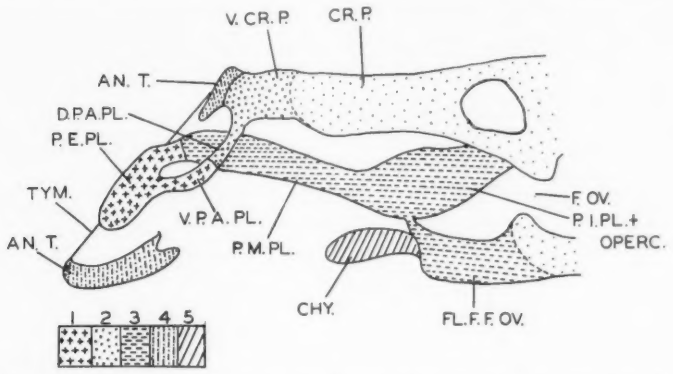

Fig. 44. Diagrammatic representation of the dorsal elements of the hyoid arch of the adult. Front view. F.OV., fenestra ovalis. 1. epihyal (V.P.A.PL., ventral portion of the processus ascendens partis externae plectri; P.E.PL., pars externa plectri). 2. suprapharyngohyal (D.P.A.PL., dorsal portion of the processus ascendens partis externae plectri; V.CR.P., lateral (visceral) portion of the crista parotica). 3. infrapharyngohyal (FL.F.F.OV., floor of the fossa fenestrae ovalis; P.I.PL.+OPERC., pars interna plectri and operculum; P.M.PL., pars media plectri). 4. stylohyal (?) (AN.T., anulus tympanicus). 5. ceratohyal (CHY.)

process represents the suprapharyngohyal or a derivative of it. (See Figs. 43 & 44).

B. THE SOUND-CONDUCTING APPARATUS

The skeletal portion of the anuran sound-conducting apparatus usually consists of an operculum which fits into the posterior portion of the fenestra ovalis, and a rod-like plectrum, which stretches between the anterior part of the fenestra ovalis and a laterally situated tympanic membrane stretched on a cartilaginous ring, the anulus tympanicus, which in certain species is dorsally incomplete.

The plectrum is absent in certain forms, such as *Ascaphus* (DE VILLIERS, 1934; VAN EEDEN, 1951), *Leiopelma* (WAGNER, 1934; E. M. & N. G. STEPHENSON, 1951), *Bombina* (STADTMÜLLER, 1931; SLABBERT, 1945), *Melanobatrachus* and *Hoplophryne* (PARKER, 1934), *Brachycephalus* (MCLACHLAN, 1943) and *Hemisus* (DE VILLIERS, 1931). An operculum is lacking in the aglossal genera *Hemipipa* (PATERSON, 1955), *Pipa* (VAN SETERS, 1922) and *Hymenochirus* (VAN SETERS, 1922). DE VILLIERS (1932) showed that *Xenopus* has a small operculum. When present, the anuran operculum is the first element of the sound-conducting apparatus to develop in ontogeny.

In *Heleophryne* the operculum makes its appearance prior to metamorphosis. In stage 1 it is still absent, and the fenestra ovalis is covered by a relatively thin membrane. In stages intermediate between 1 and 2 mesenchymatous cells, which seems to be liberated from the ventral edge of the fenestra ovalis, start to accumulate in a fairly thick layer on the outer surface of this membrane. The oper-

culum chondrifies in the posterior portion of this layer. This is in accordance with conditions obtaining in developmental stages of *Ascaphus* where VAN EEDEN (1951, p. 51) points out that "The cells constituting this membrane are clearly shown to arise from the bounding cartilage of the fenestra by a process of perichondral erosion to be described in stage 3" and (p. 74). "Towards the hind end of the fenestra ovalis the perichondral erosion referred to in stage 1 is no longer restricted to the dorso-lateral surface of the ventral border but has spread slightly medially along the dorsal surface of the capsular floor".

From the above description it is clear that the operculum of *Heleophryne* and *Ascaphus* develops from cells which are liberated mainly from the ventral rim of the fenestra ovalis. BARRY (1956) states that in *Bufo* the fenestra ovalis is occluded by a mesenchyme disk and "that the medial and lateral membranes of the mesenchyme disk represent the perichondria of the erstwhile solid wall of the auditory capsule" (p. 480). As he had evidently not studied the development of this "disk", his conclusions that its medial and lateral "membranes" are continuations of the perichondria of the otic capsule cannot be accepted. It is definitely not the case either in *Heleophryne* or in *Ascaphus*.

According to VAN SETERS (1910, quoted from KRUIJTZER, 1931), the operculum in the majority of the *Urodela* develops "door uitsnijding uit den ventralen oorkapselwand". Its development follows a similar pattern in *Ambystoma* (KINGSBURY and REED, 1909) and *Salamandra* (FUCHS, 1907). According to GOODRICH (1930, p. 481) "it appears often to be not so much 'cut out' of the cartilaginous wall (HUSCHKE, 1824; REICHERT, PARKER, HUXLEY) as to grow forwards from it in the membrane closing the fenestra ovalis". In *Triturus* (KINGSBURY and REED, 1909) it appears to chondrify in the hinder part of the membrana fenestrae ovalis. An operculum is absent in the sound-conducting apparatus of the *Apoda*.

There can no longer be any reasonable doubt that the operculum of the *Anura* is homologous with that of the *Urodela*. It occupies the same position in the posterior portion of the fenestra ovalis, it affords attachment to the same muscle, the musculus opercularis, and its mode of development appears to be similar in both these amphibian orders. As a result of its development, and on account of its absence as a separate entity in all other tetrapods, it is generally regarded to be of capsular origin. As will be pointed out later, the circumstance that its constituent cells originate from the ventral rim of the fenestra ovalis has an important bearing on the problem of its homology. The establishment of a cartilaginous connexion with the dorsal rim of the fenestra ovalis must be regarded as secondary; it is probably of functional and not of phylogenetic significance.

The second middle-ear structure, the plectrum, is present in the majority of the *Anura*. It is highly developed in the adult *Heleophryne*. As in all modern *Anura* possessing a plectrum, the pars interna plectri is fused with the dorsal rim of the crista praeopercularis. Fusion between the ventral rim of the fenestra ovalis (crista praeopercularis?) and the stapes (plectrum, columella auris) ap-

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parently also occurs in *Edops* (Romer and Witter, 1942) and in *Benthosuchus* (Bystrow and Efremov, 1940). The pars externa is anchored to the crista parotica by means of a processus ascendens. In the old adult the median portion of the plectrum is ossified as a pars media plectri.

In *Heleophryne,* as in the majority of *Anura,* the plectrum makes its appearance at metamorphosis and chondrifies from two centres. The proximal anlage is in the anterior part of the membrana fenestrae ovalis, between the anterodorsal end of the operculum and the dorsal rim of the fenestra. It chondrifies in the same tissue as the operculum and is, therefore, regarded by some investigators (Fuchs, 1907; Litzelmann, 1923; Stadtmüller, 1925; Reinbach, 1950) as a derivative of the capsular wall. Its procartilaginous anterior end merges into a tract of mesenchymatous cells that passes forward and ventro-laterad towards the Eustachian tube. Towards the end of metamorphosis, chondrification, beginning from the anterior end of the pars interna, takes place in this mesenchymatous tract. Only when this part ossifies, does the designation pars media plectri become applicable to it. Although the cartilaginous precursor of the pars media develops during metamorphosis, it was impossible to establish whether the liberated cells of the destroyed posterior portion of the palatoquadrate contribute towards its formation. Since in some species, such as *Bufo* (Barry, 1956), it is formed prior to metamorphosis, the above-mentioned cells liberated during metamorphosis, cannot be its sole source.

The second anlage, the pars externa plectri and the anulus tympanicus, chondrifies in a common mesenchymatous disk which is formed by a condensation of cells proliferating from the lateral side of the palatoquadrate. This has led Reinbach (1950) to the conclusion that the pars externa is a derivative of the mandibular arch, hence his term "pars quadrata columellae". In the young adult the pars externa is in cartilaginous continuity with the cartilaginous precursor of the pars media. Of great significance is the condition in *Probreviceps,* in which the pars externa articulates with the pars media plectri (de Villiers, 1933).

It therefore appears that the pars interna et media plectri, and the pars externa plectri, originate from the ventral rim of the fenestra ovalis, and the lateral side of the larval palatoquadrate respectively. For these two portions of the plectrum Reinbach (1950) has suggested the terms "pars otica columellae" and "pars quadrata columellae". According to him the hyoid arch does not contribute towards the formation of these structures. An alternative interpretation, more in accordance with Schmalhausen's (1923, 1956) theory, that the whole plectrum is a hyoid derivative, will now be put forward.

The ontogenetical data strongly suggest that the operculum and the pars interna et media plectri of *Heleophryne* develop in tissue derived from the ventral rim of the fenestra ovalis. The same applies to the crista praeopercularis and the floor of the fossa fenestrae ovalis. Anteriorly the crista praeopercularis merges into the otic ledge which, it has been argued, is part of the infrapharyngohyal.

It is therefore suggested that during phylogeny the infrapharyngohyal has become incorporated into the ventro-lateral wall of the otic capsule. This theory of the incorporation of the infrapharyngohyal into the wall of the otic capsule is supported by conditions obtaining in sharks and rays in which HOLMGREN (1940) found that a portion of the pharyngohyal becomes incorporated into the ventro-lateral wall of the otic capsule during ontogeny. JARVIK (1954) also maintains that the otical shelf (otic ledge) in *Eusthenopteron* in an incorporated infrapharyngohyal. It is further suggested that the only reasonable interpretation of the phylogenetic data is that in the *Anura,* the otic ledge, the floor of the fossa fenestrae ovalis, the crista praeopercularis, the operculum and the pars interna et media plectri are derived from this incorporated infrapharyngohyal.

KRUIJTZER (1931) states that in *Alytes obstetricans* the ceratohyal *articulates* with the plectrum, presumably with its pars media. According to MAREE (1945) the ceratohyal articulates with the otic capsule. It is, of course, not impossible that in the specimen(s) investigated by Kruijtzer the ceratohyal did in fact articulate with the plectrum, but, as far as is known, this is not the case in other anurans. I have reexamined both series used by Maree and find that the ceratohyal is syndesmotically connected to the floor of the otic capsule.

The connexion (articulation, synchondrosis or syndesmosis) of the ceratohyal with the floor of the fossa fenestrae ovalis and the otic ledge or the floor of the otic capsule in adult *Anura* may be regarded as important morphological evidence in favour of the hyal nature of these structures. But as this connexion is patently of a secondary nature, it is devoid of any phylogenetic significance. It is, therefore, not surprising that in some forms the ceratohyal is fused with the proximal portion of the basal process; this may indicate that a small portion of the otic ledge has been incorporated into it, and in such forms the otic ledge appears to be either weakly developed or absent (author). It is also noteworthy that VAN EEDEN (1951) states that the ceratohyal is in ligamentous connexion with the postero-lateral edge of the otic ledge in the youngest larva of *Ascaphus* at his disposal.

The pars externa plectri, like the rest of the plectrum, lies morphologically ventral to the lateral head vein and hyomandibular nerve. It therefore occupies the same position, relative to the lateral head vein and the hyomandibular nerve as does the selachian hyomandibular.

According to SCHMALHAUSEN (1923) the selachian hyomandibular represents an epihyal which is articulated by means of an infrapharyngohyal with the otic capsule at a point morphologically ventral to the lateral head vein and hyomandibular nerve. He, therefore, regards the anuran pars externa plectri as the homologue of the hyomandibular of fishes which is suspended from the otic capsule by means of an infrapharyngohyal (pars interna et media plectri). However, it is by no means certain that the hyomandibular is homologous in all fishes. According to Holmgren it is not even homologous in sharks and rays. But, on the

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whole, there is good evidence, not only embryological but also palaeontological, that the hyomandibular is composed mainly of an epihyal to which has been added proximally some small portion of the pharyngohyal, and which may or may not incorporate branchial rays (HOLMGREN, 1943).

The pars externa plectri is usually fused with the distal end of the pars media. In *Heleophryne* a small distal portion of the cartilaginous precursor of the pars media plectri fails to ossify, and becomes incorporated into the pars externa plectri of the adult. The pars externa plectri of *Heleophryne,* and probably the majority of the *Anura,* therefore, appears to be an epihyal with which is fused a small portion of the infrapharyngohyal (pars media plectri). It may be of great significance for the theory of the double origin of the plectrum that in *Probreviceps* (DE VILLIERS, 1933) there is an articulation between the pars interna and the pars media plectri. According to SCHMALHAUSEN (1956) a thin layer of juvenile cartilage usually forms the border between the stapes (infrapharyngohyal) and the extracolumella (epihyal) in developmental stages of the urodelan family *Hynobiidae.*

In *Heleophryne* the processus ascendens partis externae plectri is of double origin. Its dorsal part is formed by a ventral process of the lateral portion of the crista parotica (suprapharyngohyal) and a larger ventral part is a process of the pars externa plectri itself (epihyal). It is suggested that this ventral portion represents the dorsal articular head of the epihyal, whereas the original connexion between the infrapharyngohyal and the ventral articular head of the epihyal is represented by the connexion between the distal end of the cartilaginous precursor of the pars media plectri and the pars externa plectri.

SÄVE-SÖDERBERGH (1936) compares *Rana* with the triassic stegocephalians from Spitsbergen, and comes to much the same conclusions. He is of opinion (pp. 152—153) that the anuran plectrum is derived from "the dorsal part of the hyoid arch (hyomandibular)", that its "attachment to the parotic process is the old dorsal attachment of the hyomandibular", and that its attachment to the crista praeopercularis "is the old ventral attachment of the hyomandibular".

The anulus tympanicus, as such, is a structure peculiar to the *Anura.* In *Heleophryne* it chondrifies towards the end of metamorphosis in the same mesenchymatous disk as does the pars externa plectri. Its homology is uncertain but according to GAUPP (1899) it is probably homologous with the selachian prespiracular cartilage.

HOLMGREN (1943, p. 105) summarising the development of the hyoid arch in *Salmo salar* states that "the stylohyal rudiment belongs to a layer of skeletal tissue that is different from and more superficial than that to which the hyosymplectic and the ceratohyal belong" and "it is attached to the lateral surface of the rudiment of the hyal arch proper as a lateral outgrowth of some independence. The mode of its development led to the conclusion that in *Salmo* the stylohyal may correspond fairly closely to a branchial ray belonging to the hyal

arch . . ." It is tentatively suggested that the anulus tympanicus is the homologue of the stylohyal of fishes.

The homologization of the component parts of the sound-conducting apparatus of the *Amphibia* is not an easy task. The constituent elements are probably not directly comparable with those of higher forms, such as mammals, in which their ontogenetic and phylogenetic history is well known. The problem is further aggravated by the paucity of ontogenetical data. These data are often of such a nature that they do not unequivocally lend support to either of the two main theories. According to the one theory no part of the sound-conducting apparatus is of hyoid origin; according to the other, this arch contributes in varying degree towards the formation of the plectrum.

REINBACH (1950) gives an excellent summary of the known facts and theories and concludes that in the three living orders of the *Amphibia,* the plectrum is of double origin, its proximal portion deriving from the otic capsule, and its distal portion from the palatoquadrate. However, he concedes the possibility that the greater part of the distal portion of the apodan stapes is of hyoid origin.

The latest comprehensive review of the literature relating to this problem is given by BARRY (1956) to whose paper the reader is referred for a summary of current accepted views.

From these papers it is evident that the majority of the investigators favour the theory of the nonparticipation of the hyoid arch in the development of the sound-conducting apparatus. The evidence for its hyoid derivation is scanty. MARCUS (1909) claims that the stapes of the *Apoda* is derived from the hyoid arch. As far as could be ascertained, no investigator found convincing evidence for the derivation of the sound-conducting apparatus from the hyoid arch in the urodeles, although KINGSBURY and REED (1909) state that the plectrum and the ceratohyal chondrify in a common blasteme. Apart from GAUPP's (1893) surmise and SCHMALHAUSEN's (1923) general assertion that the plectrum of the *Anura* is a hyoid derivative, the only specific works supporting this theory are those of SALVADORI (1928) and GAZAGNAIRE (1932). The former found that a transient ligament connects the ceratohyal with the pars externa plectri in *Rana* and in *Bufo*. GAZAGNAIRE (1932), working on *Rana fusca* confirmed Salvadori's conclusions.

The theory regarding the homologies of the plectrum put forward in this paper can be summarised as follows: The infrapharyngohyal has, like the pharyngohyal element in sharks and rays (HOLMGREN, 1940, 1943), become incorporated into the lateral wall of the otic capsule ventrally to the fenestra ovalis. In adult *Heleophryne* it gives rise to the otic ledge, the floor of the fossa fenestrae ovalis, the crista praeopercularis, the operculum and the pars interna et media plectri. The pars externa plectri represents mainly an epihyal, and the processus ascendens partis externae plectri its dorsal articular head. The anulus tympanicus is probably the homologue of the stylohyal of bony fishes. (See Figs. 43 & 44).

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Aufbau des Panzers obersilurischer Heterostraci und Osteostraci Norddeutschlands (Geschiebe) und Oesels

von

WALTER GROSS

(Eingegangen Juni 30, 1960)

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Einleitung

Die fischführenden Schichten des Beyrichienkalks norddeutscher Geschiebe sind besonders reich an Schuppen von Thelodontiern und Acanthodiern, Reste von Heterostraci sind ungleich viel seltener, und sichere Osteostraci-Reste sind bisher noch nicht erwähnt worden. Die von BROTZEN (1933, 1934 a, 1934 b) und GROSS (1947) beschriebenen Schuppen und Knochenreste sind alle durch mühsame Nadelpräparation gewonnen worden. 1952 begann ich, die fischführenden Geschiebe nach der bekannten Methode in Essigsäure aufzulösen, wobei sich der Anfall gut erhaltener Schuppen und Panzerbruchstücke gegen die bisherige Ausbeute unvergleichlich erhöhte. Erst jetzt fanden sich auch viel mehr Reste von Panzern und Schuppen verschiedener Gattungen der Heterostraci und Osteostraci. Eine Neubearbeitung wurde erforderlich. Im Zusammenhang mit der Untersuchung des Porenkanalsystems in der Oberschicht des Exoskelettes verschiedener Agnathen und Fische zog ich bereits 1956 die Schuppen von *Poracanthodes* heran und ferner Knochenplättchen incertae sedis,

von denen ich nicht sicher entscheiden konnte, ob sie von *Poracanthodes* oder von Cephalaspiden stammen. Neues Material brachte die Entscheidung; im Frühjahr 1957 fanden sich im Auflösungsrückstand eines Geschiebes mehrere fast intakte Schuppen eines Cephalaspiden, die die Oberschicht und das Porenkanalsystem der als Knochenplättchen incertae sedis beschriebenen Reste aufwiesen. Bei einem Besuch in Stockholm im Juni 1957 legte ich meine Schliffe Dr. Ørvig vor, der über reichliches Cephalaspiden-Material verfügt. Dr. Ørvig bestätigte sofort die Richtigkeit meiner auf Grund der neuen Funde geäußerten Vermutung und wies auf Abbildungen bei WÄNGSJÖ (1952) hin, die mit einzelnen Resten des neuen Fundes übereinstimmen.

In Stockholm hatte ich auch die Gelegenheit, viel Heterostracen-Material zu sehen, das mir bisher nur aus der Literatur bekannt war. Die Auflösung des Geschiebes, aus dem Brotzen sein Material erlangt hatte, brachte eine Fülle von kleinen Heterostracen-Bruchstücken zum Vorschein, die noch weit an Anzahl übertroffen wurden von Resten aus einem ähnlichen Geschiebe. Beide Geschiebe sind vom verstorbenen Berliner Sammler H. Müller, Friedenau, in Berliner Raum gefunden worden und tragen nun die Sammlungs-Nummern Bey 36 (Material Brotzen) und Bey 37. Diese Geschiebe enthalten eine Fischfauna, in der *Thelodus parvidens* fehlt, dafür aber *Thelodus (Turinia?)* cf. *scoticus* reichlich vorhanden ist. Die Acanthodier sind die gleichen wie in den übrigen Geschieben des Beyrichienkalks, aber neu sind die meisten nachfolgend beschriebenen Heterostraci und Osteostraci; nur sehr spärlich finden sich in einigen weiteren Geschieben die Reste von *Traquairaspis* und *Zenaspis?* sp. indet. Diese letzteren Geschiebe sind dolomitische Gesteine, die vielfach keine Invertebraten-Rest enthalten und durch die große Anzahl der Schuppen von *Thelodus (Turinia?)* cf. *scoticus* gekennzeichnet sind. In den vom Sammler H. Müller als devonisch bezeichneten Geschieben fehlen Invertebraten-Reste, die Fischfauna ist ähnlich der der eben erwähnten dolomitischen Geschiebe, aber besonders gekennzeichnet durch den Reichtum an Heterostraci- und Osteostraci-Resten, die nachfolgend beschrieben werden. Alle erwähnten Gesteine sind Kalke, bei den Geschieben Bey 36 und 37 ist der Kalk rot gefärbt, konglomeratisch und mit einer geringen Beimengung von Quarzsand. Ich hoffe, daß zur Altersfrage dieser sicher über den echten Beyrichienkalken liegenden Gesteine demnächst Dr. Ørvig Stellung nehmen wird.

Das aus den Geschieben Bey 36 und 37 gewonnene Material eignet sich dank ausgezeichneter Färbung hervorragend für histologische Untersuchungen. Bisher sind nur wenige Heterostraci eingehend histologisch untersucht worden, an ihrer Spitze die Gattungen *Psammolepis, Psammosteus, Pteraspis* und *Pycnaspis*. Viele weitere Gattungen sind zwar ebenfalls untersucht worden (BROTZEN 1934 a, KIAER und HEINTZ 1935, GROSS 1947, BYSTROW 1955), doch nicht so genau wie die Psammosteiden und Pteraspiden; man hat auch die Frage der Bildungsweise des Skelettes dieser Gattungen zu wenig berücksichtigt. Das versucht nun

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die vorliegende Arbeit für das Material aus dem Beyrichienkalk und einige Reste aus dem Oberludlow von Oesel (Ohesaare-Pank) nachzuholen.

Nachdem sich die Knochenplättchen incertae sedis (Gross 1956) als Reste einer Osteostracen-Gattung erwiesen haben, wurde auch eine erneute Bearbeitung dieser Reste erforderlich. Dabei ergänzte die Untersuchung der Bruchstücke mit dem binokularen Mikroskop aufs beste die Untersuchung der Dünnschliffe. Auch hier stand die Bildungsweise der Oberschicht und die Einschließung des Porenkanalsystems in die Oberschicht im Vordergrund der Erforschung. Ferner waren Reste einer weiteren, nicht näher bestimmbaren Osteostraci-Gattung zu berücksichtigen.

Von besonderem Interesse war für mich das Porenkanalsystem und die Skulpturen der Osteostraci, die ich bisher nur an Arten der Gattung *Trematapis* näher untersuchen konnte. Der Hinweis von Denison (1951 b) und Bölau (1951), daß auch die Gattung *Dartmuthia* im Porenkanalsystem Siebplatten besitzt, regten mich dazu an, diese Gattung auch in den Kreis der Betrachtung zu ziehen, was mir durch einige, teils käuflich erworbene, teils geschenkte Reste möglich wurde. Überraschend bei der Untersuchung der Osteostraci-Reste waren die Ergebnisse über die vielfach sich wiederholende Mesodentin-Bildung der Skulpturen. Ähnliche Beobachtungen machte ich auch bei einer Gattung der Heterostraci. So stand der Aufbau der Oberschicht aller untersuchten Gattungen im Mittelpunkt der Fragestellung.

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Meine Untersuchungen sind sehr gefördert worden durch die Unterstützung mit Material und Vergleichsstücken, die ich meinem Freunde Dr. Ørvig verdanke. Herrn Dr. Ørvig möchte ich auch besonders danken für die Gelegenheit zu vielfacher Aussprache über histologische Fragen und für die Erlaubnis, seine hervorragende Schliffsammlung zu studieren. Ebenso danke ich Herrn Prof. Dr. Stensiö für die Unterstützung meiner Studien in Stockholm und vor allem für ihre Ermöglichung. Jeder Besucher der Paläontologischen Abteilung des Naturhistorischen Reichmuseums in Stockholm wird sich immer wieder gerne der großzügigen und herzlichen Gastfreundschaft erinnern, die er dort findet. — Für die mit der Auflösung der Gesteine in Essigsäure verbundenen Arbeiten danke ich auch an dieser Stelle dem Oberpräparator Herrn F. Marquardt.

Das Auslesen des Materials führte ich aus begreiflichen Gründen selber durch. Um die teure Reproduktion von Photographien zu sparen, habe ich alle Abbildungen als Strichzeichungen angefertigt. Einige schematische Abbildungen sollen die Zeichungen nach den Originalen ergänzen. Ich bitte zu berücksichtigen, daß ich kein geborener Zeichner bin; die Herstellung der Zeichnungen nimmt sehr viel Zeit in Anspruch, und das Ergebnis entspricht leider nicht den Vorstellungen.

Walter Gross

Heterostraci

Die fischführenden Beyrichienkalke sind überaus reich an *Thelodus*- und Acanthodier-Schuppen. Die wahrscheinlich unteren Beyrichienkalke sind durch *Thelodus parvidens* gekennzeichnet, die oberen durch *Thelodus (Turinia?)* cf. *scoticus*. Beide Arten schließen sich aus. Die Acanthodier geben keine Leitformen ab. Überall im Beyrichienkalk finden sich — wenn auch nur sehr zerstreut — Reste der Heterostracen-Gattung *Oniscolepis* Pander, zu der ich jetzt alle von mir früher (Gross 1947) als *Strosipherus* Pander beschriebenen Reste stelle. Auch vereinige ich jetzt — ebenso wie bereits Rohon (1893) — beide genannten Gattungen Panders unter dem Namen *Oniscolepis*, da sich diese Gattung häufig in der bekannten Typuslokalität Ohesaare-Pank auf Oesel findet und jederzeit zum Vergleich herangezogen werden kann.

In den roten, ein wenig Quarzsand führenden Geschieben Bey. 36 und 37, die das meiste Material für die vorliegende Arbeit geliefert haben, fehlt *Oniscolepis* gänzlich; dafür treten nun ganz andere Gattungen auf, die das j ü n g e r e A l t e r dieser Gesteine bezeugen. Am häufigsten ist die Gattung *Traquairaspis*, die bisher von Brotzen und Gross als *Orthaspis* Brotzen beschrieben worden ist. Ihre Reste sind leicht zu erkennen. Vereinzelt finden sich schon Bruchstücke dieser Gattung in den oberen dolomitischen Beyrichienkalken, so z. B. im Geschiebe Bey. 6, aber häufig sind die Panzerreste von *Traquairaspis* nur in den genannten rotbunten Kalken. Nur in letzteren Geschieben finden sich die Gattungen *Anglaspis* und *Corvaspis*, *Anglaspis* recht häufig, *Corvaspis* nur vereinzelt. Beide Gattungen sind leicht zu erkennen. Manche Reste von *Corvaspis* erinnern an *Oniscolepis*, vielleicht bestehen nähere Beziehungen zwischen beiden Gattungen.

Im Beyrichienkalk finden sich sehr selten Reste mit dicht aneinanderschließenden Dentinleisten, die am ehesten mit *Tolypelepis* Pander zu vergleichen sind. Das Material ist zu gering für eine Untersuchung und sichere Bestimmung; auch fehlt es mir an sicher bestimmtem Vergleichsmaterial der Gattung *Tolypelepis*, deren Reste vom Ohesaare-Pank auf Oesel stammen.

TRAQUAIRASPIS SP. INDET.

Die Gattung *Traquairaspis* wurde 1932 von Kiaer für die 1913 von Traquair als *Cyathaspis cambelli* beschriebene Heterostraci-Art aus Schottland errichtet. White erkannte 1948, daß zu *Traquairaspis* auch die von Wills 1935 aufgestellte Gattung *Phialaspis* aus Südengland gehört, die ursprünglich als *Cythaspis symondsi* Lankester (1864) beschrieben worden war. Zu *Traquairaspis* stellt White (1948) demnach drei Arten: *Tr. cambelli* (Traq.), *Tr. symondsi* (Lank.) und *Tr. pococki* (White 1946).

Wie ich mit freundlicher Hilfe von Dr. Ørvig, Stockholm, auf Grund neuen Materials feststellen konnte, gehört zur Gattung *Traquairaspis* auch die 1934 von

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Brotzen aufgestellte Gattung *Orthaspis*. 1947 hatte Gross nachgewiesen, daß mit *Orthaspis plana* Brotzen auch die Gattung *Lophaspis* Brotzen und die irrtümlich zu *Lophosteus* Pander gestellte Art *Lophosteus mutabilis* Brotzen vereinigt werden müssen. Diese *Traquairaspis*-Reste aus den norddeutschen Geschieben können vorläufig nicht als *Traquairaspis plana* (Brotzen) beschrieben werden, denn die Speziesmerkmale der bisher monotypischen Gattung fallen mit den Gattungsmerkmalen von *Traquairaspis* zusammen. Die kleinen Bruchstücke der Geschiebe bieten vorerst keine Grundlage für die Bestimmung einer Art; der Speziesname *plana* muß daher einstweilen außer Gebrauch treten, da es noch keine Definition für eine besondere Art aus den Geschieben gibt. Die Reste aus den Geschieben bezeichne ich als *Traquairaspis* sp. indet., denn es kann auch nicht der Nachweis geführt werden, daß sie mit einer der Arten aus Großbritannien identisch sind.

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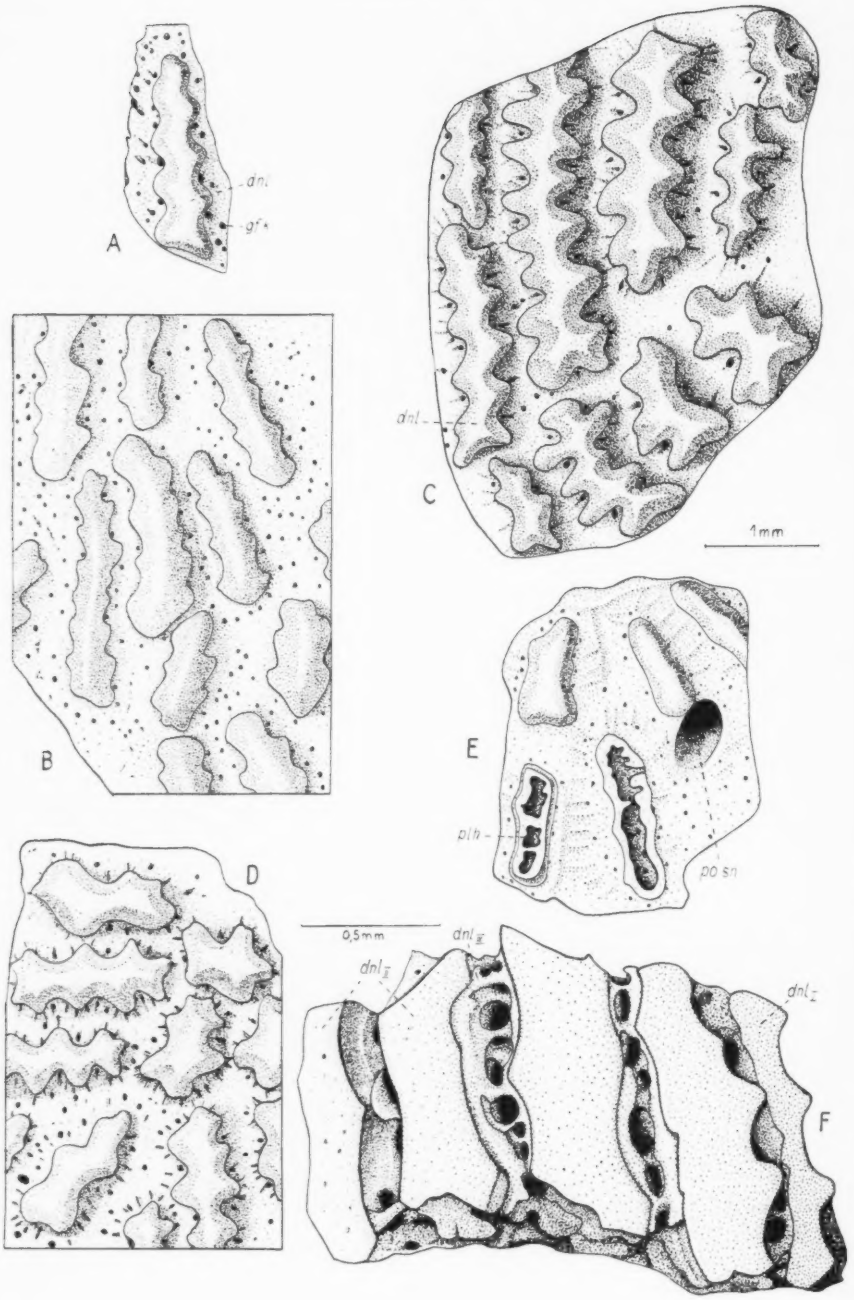
Die Gattung *Traquairaspis* umfaßt demnach drei wohlumgrenzte Arten: *Tr. cambelli* (Traq.), *Tr. symondsi* (Lank.) und *Tr. pococki* (White); dazu kommt *Traquairaspis* sp. indet. aus norddeutschen Geschieben anstelle der früher von Brotzen auf drei Gattungen verteilten Arten: *Orthaspis plana, Lophaspis crenulata* und *Lophosteus mutabilis*.

Das Material. Nur in zwei von Herrn H. Müller, Friedenau, in den dreißiger Jahren gesammelten Geschieben finden sich zahlreiche Bruchstücke des Panzers dieser Gattung, deren Skulptur und histologische Struktur sehr gut erhalten sind. Eines dieser Geschiebe, das nun die Verzeichnisnummer Bey. 36 enthält, lag den Untersuchungen von Brotzen (1933, 1934 a und 1934 b) und Gross (1947) zugrunde. Viel mehr und noch besser erhaltene Bruchstücke lieferte das andere Geschiebe mit der Verzeichnisnummer Bey. 37. Zur näheren Beschreibung dieser Geschiebe und ihrer Fischreste sei auf S. 74 verwiesen. Nur sehr wenige weitere Geschiebe enthielten Reste dieser Gattung.

Die Bruchstücke des Panzers von *Traquairaspis* sind recht groß und oft auffallend dick, namentlich wenn sie vom Rande der Panzerplatten stammen. Meist sind sie hellgelblich oder weißlich gefärbt, mit rot oder violett ausgefüllten Kanälen und Hohlräumen. Oft heben sich die charakteristischen Skulpturen durch intensiv gelbe Färbung scharf von dem helleren Aspidin ab. Die aus Dentin bestehenden Skulpturen können auch ganz durchsichtig sein, so daß man ihren Gefäßplexus bereits im auffallenden Licht leicht sehen kann. An den Skulpturen ist die Gattung fast immer mühelos zu erkennen.

Der Aufbau der Reste. Wie bei den meisten Platten und Schuppen der Heterostraci können wir auch hier drei Schichten erkennen: eine Oberschicht, die die Skulpturen liefert, eine spongiöse oder gekammerte Mittelschicht und eine fast dichte Unterschicht. Das Zentrum der Ventralplatte weist keine Skulpturen auf, es ist glatt. Der größte Teil der Panzerplatten hat eine großkammerige Mittelschicht. Die Sinneskanäle liegen in der Mittelschicht und entsenden Zweigkanäle, die auf der Oberfläche münden (Abb. 1 E). Die Oberschicht ist eigent-



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lich keine zusammenhängende Schicht, da sie meist aus wohlgetrennten Skulpturen besteht, zwischen denen die Mittelschicht mit zahlreichen Blutgefäß-Mündungen an die Oberfläche tritt. Ist die Oberschicht als geschlossene Dentindecke entwickelt, etwa im Zentrum der Ventralplatte, so bildet sie eigentlich nur den oberen Abschluß der Spongiosakammern der Mittelschicht.

Die Skulpturen der Oberschicht (Abb. 1). Die sehr charakteristischen Skulpturen (*dnl*) sind meist als isolierte, langgestreckte und hohe Wälle entwickelt, die oft durch sehr kräftige Seitenzacken (Abb. 1 C) ausgezeichnet sind. Vielfach sind die Hinterenden der Wälle breiter und etwas höher als die Vorderenden, auch sind die Seitenzacken überwiegend ein wenig nach vorne gerichtet (Abb. 1 A und B). Ein großer Teil der Reste läßt sich nach diesem Merkmal orientieren. Im Bereich des Vorderendes der Platten versagt dieses Merkmal jedoch meist, da die Skulpturen hier parallel zum Außenrand der Platten verlaufen, das heißt quer zu deren Längsachse. Dort finden sich dicht nebeneinander quer und längsverlaufende Wälle (Abb. 1 D). In bestimmten Regionen werden die Wälle sehr kurz und nehmen fast tuberkelförmige Gestalt an. Die Abb. 1 gibt nicht im entferntesten alle Möglichkeiten der Ausbildung wieder.

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Die Skulpturen sind meist glänzend. Stets sind sie durch eine ausgeprägte feine Furche von der Oberfläche der Mittelschicht sehr scharf abgesetzt; es sieht so aus, als ob die Skulpturen aus der Mittelschicht hervorbrächen. In der Abb. 1 sind diese Furchen nur als einfache ausgezogene Linien dargestellt, am Objekt selber oder in Photographien treten sie deutlich hervor. So wie die Wälle in der Breite und Höhe, in der Zackung und in der Kantenbildung ungemein variabel sind, so wechselt auch der Abstand der Wälle. Die Wälle können so dicht angeordnet sein, daß nur eine Reihe von Blutgefäßkanälen (*gfk*) zwischen ihnen münden kann, oder sie liegen weit getrennt. Auf kürzeste Entfernung kann der Abstand wechseln. Nie aber verschmelzen die Wälle miteinander; Verzweigungen der Skulpturen sind selten. Brechen die Skulpturen ab, so liegen die engen Blutgefäßkanäle oder — bei erst eben gebildeten Wällen — weite Hohlräume offen (Abb. 1E, *plh*). Die Oberfläche der Mittelschicht ist zwischen den Skulpturen meist nicht eben, sondern ein wenig eingesenkt und im Zusammenhang mit dem Verlauf der Blutgefäße etwas gefurcht.

Abb. 1. *Traquairaspis* sp. indet. A—E Bruchstücke des Panzers mit typischen Skulpturen (Dentinleisten); × 15. A Dentinleiste mit verbreitertem Hinterende; f 650 Berlin. B Lange Dentinleisten mit nach vorne gerichteten Seitenzacken; f 651 Berlin. C Dentinleisten mit besonders langen Seitenzacken; f 652 Berlin. D Rest vom Vorderende des Panzers mit rechtwinklig zueinander gerichteten Dentinleisten; f 653 Berlin. E Rest mit der Mündung eines Zweigkanals der Sinneslinie; die abgebrochenen jungen Dentinleisten zeigen weite Hohlräume; f 654 Berlin. F Bruchstück einer Schuppe (?) mit zwei Generationen der Dentinleisten, die resorbierte Oberfläche der 2. Generation weist auf das ehemalige Vorhandensein einer dritten Gnerationen hin; × 40; f 655 Berlin. *dnl* Dentinleiste; dnl_{I-III} Dentinleiste der ersten bis dritten Generation; *gfk* Mündung von Gefäßkanälen; *plh* Pulpahöhle; *po.sn* Mündung eines Sinneskanals.

Die Sinneskanäle münden schräg aufsteigend hinter, vor oder seitlich von den Skulpturen mit kreisrunder, längsovaler oder querovaler Öffnung (Abb. 1 E, *po.sn*). Stets ist der Vorderrand der Mündung steil abfallend, der Hinterrand allmählich auslaufend, eine Eigentümlichkeit, die sich bei allen Agnathen und Fischen findet, bei den Dipteriden sogar an den Porenkanälen. Die Zweigkanäle der Sinneslinien verlaufen schräg, quer oder längs unter den Skulpturen in der Mittelschicht. Ist die Mittelschicht dick, so liegen die Sinneskanäle in ihrer oberen Hälfte.

Einige wenige Reste zeigen mehrfache Bildung der Skulpturen in auffallender Regelmäßigkeit (Abb. 1 F). Der abgebildete Rest weist zwei Skulptur-Lagen (*dnl I—II*) übereinander auf, aber allem Anschein nach bestand noch eine dritte Lage (*dnl III*) darüber, wie weiter unten (S. 88) beschrieben wird. Die jüngeren Skulpturen sind breiter und höher als die überlagerten, deren Verlauf sie genau folgen. Die Furchen zwischen den Skulpturen der oberen Lage sind mit einem trübweißen Dentin (*dnl III*) ausgefüllt, durch das unregelmäßig Gefäßkanäle aufsteigen. Dieses Dentin gehörte vermutlich zur dritten, nicht mehr vorhandenen Skulptur-Lage (Abb. 3 E). Der stark gewölbte Rest stammt vielleicht von einer Schuppe.

Der Aufbau der Mittelschicht kann sehr verschieden sein und darf nicht unkritisch in die Diagnose der Gattung aufgenommen werden. An den dicken Stellen des Panzers, zum Beispiel an den Rändern, ist die Mittelschicht rein spongiös (reticulär) entwickelt, erfüllt von vielen Lagen enger Gefäßkanäle, deren Mündungen auf der Oberfläche der Mittelschicht zwischen den Skulpturen zu sehen sind. Die dünneren Reste haben fast stets eine großkammerige (cancellare) Mittelschicht, die für viele Heterostraci so ungemein typisch ist. Eine derartige Mittelschicht findet sich anscheinend in größerem Umfang als die reticuläre Spongiosa.

Ein großes zentrales Feld des Ventralpanzers ist frei von Skulpturen, aber auch frei von Mündungen der Gefäßkanäle der Mittelschicht. Die weiten Kammern der Mittelschicht werden oben nicht von einer Aspidinschicht abgeschlossen, sondern von einer dichten Dentinschicht, die je nach dem Bildungsalter dünn oder dick sein kann. Diese Verhältnisse werden weiter unten (S. 85) beschrieben.

Auch die Unterschicht (Basalschicht) wechselt sehr in der Dicke. Sie ist fein lamellär, nur von sehr wenigen aufsteigenden Blutgefäßen durchbohrt, ziemlich eben und geht unmittelbar in die Mittelschicht über.

Maße. Reste mit stark entwickelter Mittelschicht können bis 3 mm dick werden, Reste mit einfacher Kammerspongiosa sind dagegen meist nur an 0,5 mm dick. Die Länge der Skulpturwälle kann von 0,5 bis 2 mm reichen; ihre Höhe beträgt nicht selten 375 μ; die Breite schwankt zwischen 50 μ und 875 μ. Selbst die Seitenzacken breiter Wälle erreichen eine Länge von 200 μ. Die Mündungen der Gefäßkanäle an der Oberfläche der Mittelschicht zwischen den Wällen

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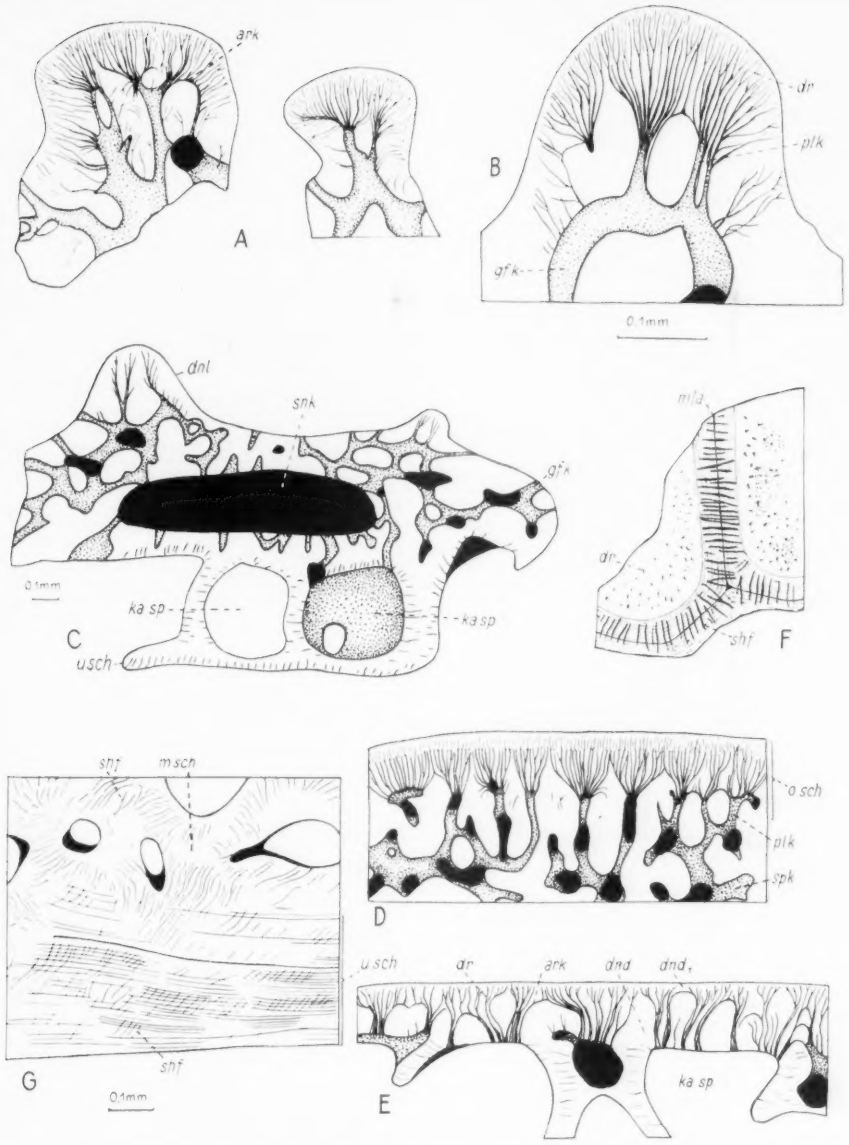
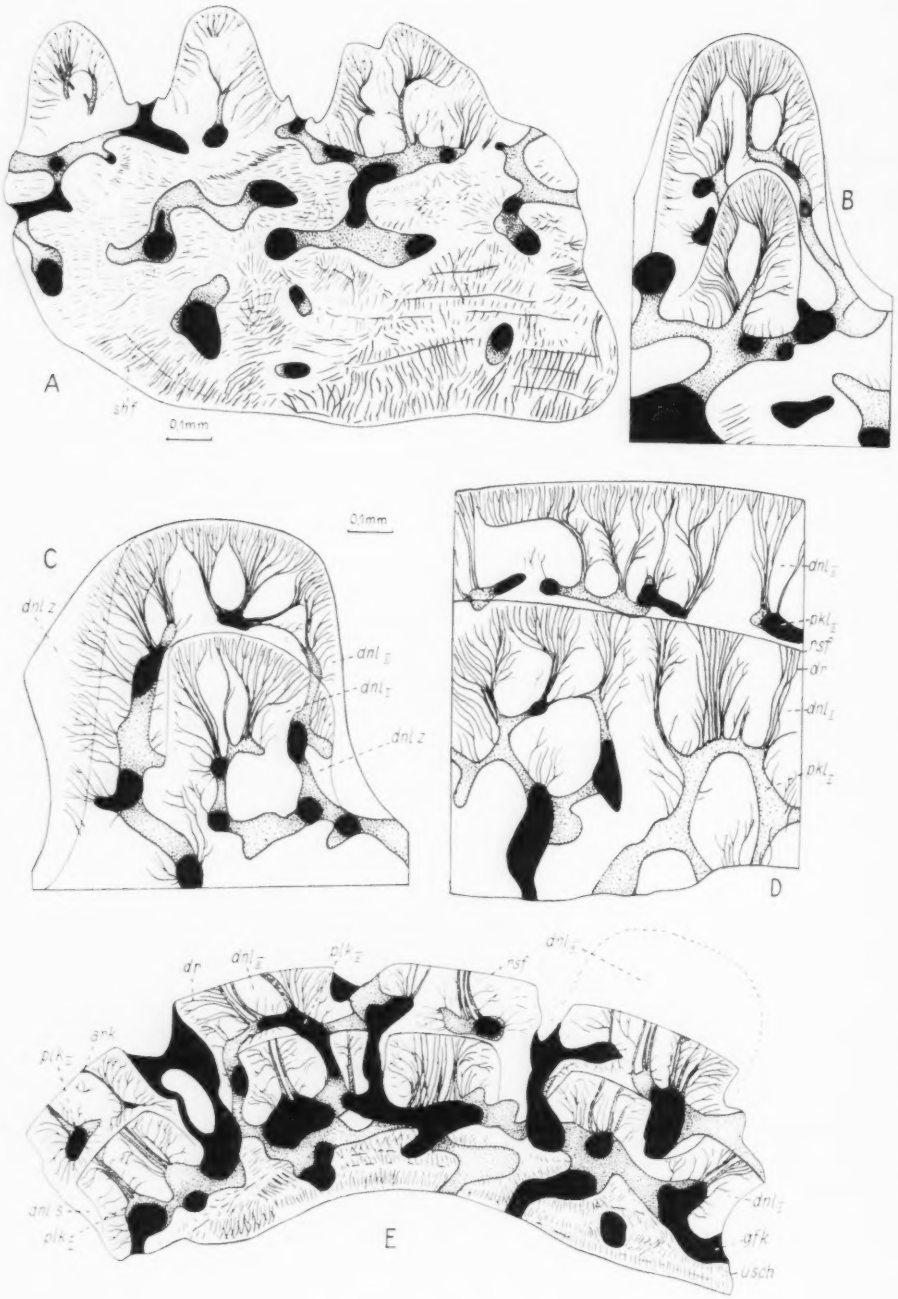


Abb. 2. *Traquairaspis* sp. indet. Dünnschliffe durch den Panzer. A Schliff Nr. 2137 Berlin; vertikaler Querschliff durch Dentinleise; × 65. B Schliff Nr. 2138 Berlin; vertikaler Querschliff durch Dentinleiste; × 125. C Schliff Nr. 2630; Vertikalschliff durch den Panzer mit schräg getroffenem Sinneskanal; × 38. D Schliff Nr. 2154 Berlin; vertikaler Längsschliff durch Dentinleiste; × 65. E Schliff Nr. 2626 Berlin; Vertikalschliff durch das Mittelfeld des Ventralpanzers mit geschlossener Dentindecke; × 65. F Schliff Nr. 2168 Berlin; Horizontalschliff durch Dentindecke des Ventralpanzers; × 65. G Schliff Nr. 2135 Berlin; Vertikalschliff durch die Unterschicht; × 65. *ark* Arkadenkanal; *dnd* Dentindecke; *dnd*$_1$ oberste Lage der Dentindecke; *dnl* Dentinleiste; *dr* Dentinröhrchen; *gfk* Gefäßkanal; *ka.sp* Spongiosakammer; *mla* Mittellamelle; *msch* Mittelschicht; *osch* Oberschicht; *plk* Pulpakanal; *shf* Sharpeysche Fasern; *snk* Sinneskanal; *spk* Spongiosakanal; *usch* Unterschicht.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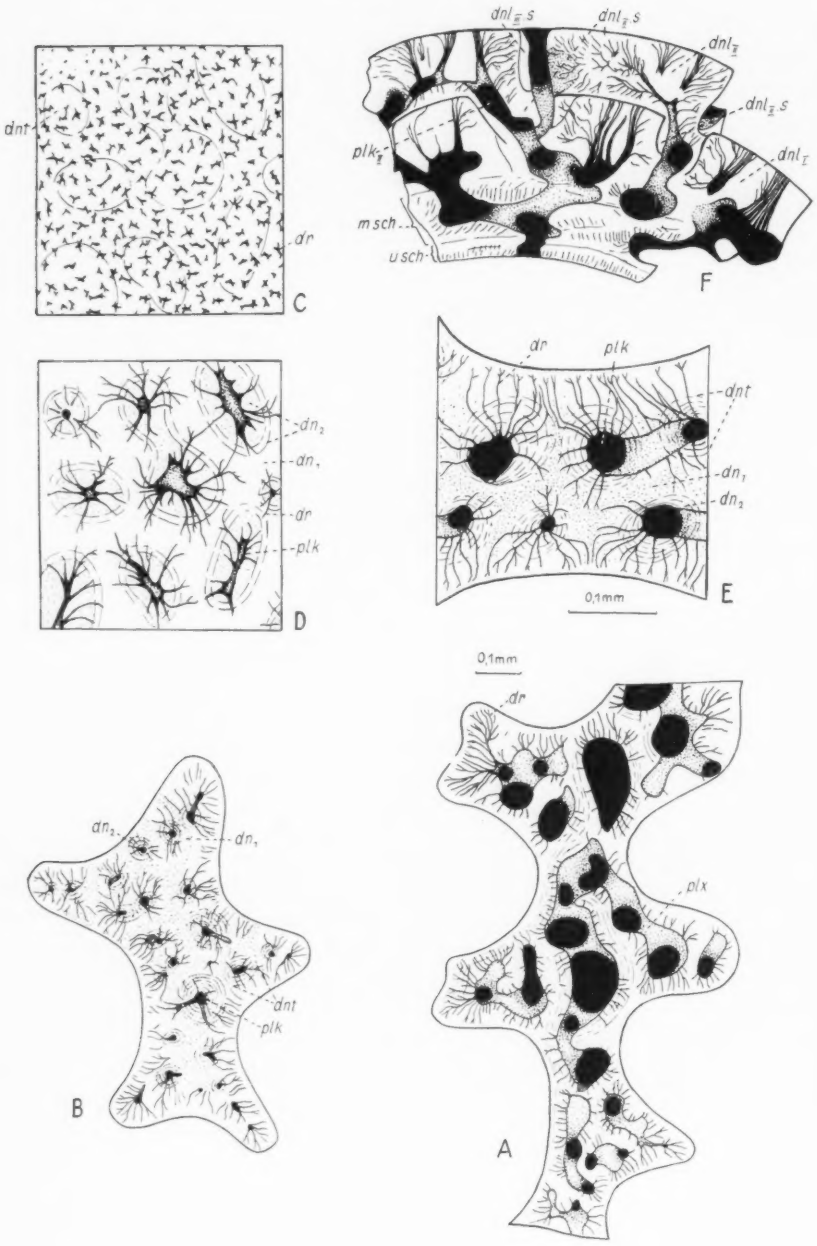
haben einen Durchmesser von meist 25 μ. Die Breite der Sinneskanalmündungen schwankt zwischen 250 und 500 μ. Der Durchmesser der Spongiosakammern variiert um 500 μ; die Poren zwischen den Kammern haben einen Durchmesser von 50 μ.

Histologie (Abb. 2—4 u. 8 E). Wie bei allen Heterostracen ist auch der Panzer von *Traquairaspis* aus Dentin und Aspidin aufgebaut; aus Dentin bestehen die Skulpturen und die glatte, dichte Oberschicht im zentralen Feld der Ventralplatte, aus Aspidin die reticuläre oder cancelläre Mittelschicht und die Unterschicht. Dentin und Aspidin können deutlich eine sehr feine Lamellierung zeigen, deren Sichtbarkeit im Aspidin aber meist durch zahlreiche Bündel Sharpeyscher Fasern (*shf*) gestört wird.

Die Skulpturen. Im Gegensatz zu den Cyathaspida und Pteraspida haben die Skulpturen von *Traquairaspis* so weite Abstände, daß sie keine geschlossene Schicht bilden; es fehlen daher zwischen ihnen die engen Rinnen (*zwr*) mit ihrem charakteristischen Querschnitt. Nicht selten sitzen die Dentinskulpturen einem niedrigen Aspidinsockel auf, der mit seinen Gefäßkanälen noch zur Spongiosa gehört. Aus den Spongiosakanälen erhebt sich ein horizontal ausgebreitetes Netz enger subepidermaler Gefäße, die durch Schlingen und Randarkaden verbunden sind (Abb. 4 A). Das Gefäßnetz entsendet senkrecht oder ein wenig schräg nach oben, oft in der Längsrichtung, sehr regelmäßig parallel angeordnete Pulpakanäle (*plk*). Aus diesen und ihren sehr dünnen arkadenförmigen Endverbindungen (*ark*) strahlen nun die Dentinröhrchen (*dr*) zur Oberfläche der Skulpturen (Abb. 2 A, B und D; Abb. 3; Abb. 4 A und B). Anstelle der engen aufsteigenden Pulpakanäle sieht man nicht selten dichte Bündel langer Dentinröhrchen, die auch die bogenförmigen Verbindungsarkaden bilden (Abb. 3 B—E). In einem gewissen Abstand von der Oberfläche lösen sich die Dentinröhrchen in ein Büschel feiner Endästchen auf, meist so gleichmäßig, daß eine charakteristische helle Durodentinschicht entsteht. Man kann daher vielfach drei Zonen oder Schichten im Dentin unterscheiden. Zu unterst eine meist sehr deutlich lamelläre Zone, die sich vom Aspidin kaum unterscheidet; sie schließt die engen Pulpakanäle bzw. die langen unverzweigten Dentinröhrchen bis zur Höhe der Arkadenverbindungen ein (Abb. 3 B, D). Es folgt über den Arkadenverbindungen bis zu der pinselartigen Verzweigung der Dentinröhrchen

Abb. 3. *Traquairaspis* sp. indet. Dünschliffe durch den Panzer; × 65. A Schliff Nr. 2131 Berlin; vertikaler Querschliff durch den Panzer. B Schliff Nr. 2628 Berlin; vertikaler Querschliff durch zwei Dentinleisten-Generationen. C Schliff Nr. 2628 Berlin; vertikaler Querschliff durch zwei Dentinleisten-Generationen, links Seitenzacke der jüngeren Dentinleiste. D Schliff Nr. 2629 Berlin; vertikaler Längsschliff durch zwei Dentinleisten-Generationen. E Schliff Nr. 2627 Berlin; vertikaler Querschliff durch Schuppe (?) mit zwei bzw. drei Dentinleisten-Generationen; vgl. Abb. 1 F. *ark* Arkadenkanal; *dnl$_{I-III}$* Dentinleisten der ersten bis dritten Generation; *dnl.s* Sockel der neuen Dentinleiste; *dnl.z* Seitenzacke der Dentinleiste; *dr* Dentinröhrchen; *gfk* Gefäßkanal; *plk$_{I-II}$* Pulpakanal; *rsf* Resorptionsfläche der Dentinleisten; *shf* Sharpeysche Fasern; *usch* Unterschicht.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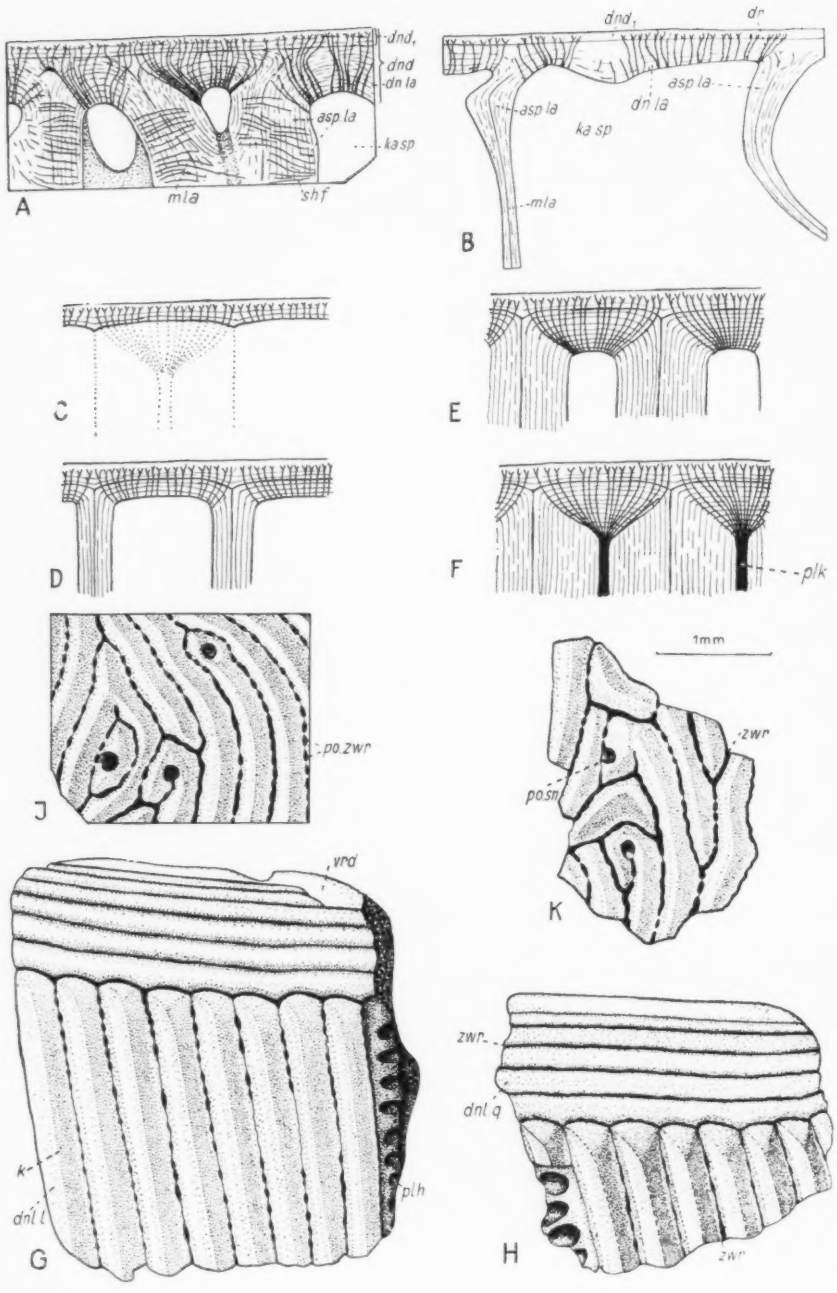
eine etwas weniger deutlich lamellär ausgebildete Dentinschicht, der eigentliche Dentinmantel der Skulpturen. Die dritte und oberste Schicht (Abb. 3 A—E) ist hell, nicht sichtbar lamellär, durodentinartig; ihre Härte bedingt den Glanz der Skulpturen.

Die unterste der drei eben beschriebenen Schichten des Dentins geht kontinuierlich in das feinlamelläre Aspidin über, dem die Dentinröhrchen fehlen. Gelegentlich geben die Kanäle des subepidermalen Plexus auch Dentinröhrchen nach unten ab (Abb. 3 E), die dann stets sehr unregelmäßig und wirr verlaufen. Dieselbe Erscheinung findet sich im Dentin aller Agnathen und Fische, sobald die Dentinröhrchen nicht nach oben oder zu den Seiten, sondern nach unten entsandt werden. Die feine Lamellierung des Dentins geht völlig ohne Unterbrechung in die des unterlagernden Aspidins über, was noch dadurch unterstrichen wird, daß sich im obersten Aspidin gelegentlich verstreute Dentinröhrchen finden. Die Schichtbildung des Dentins tritt in vertikalen Längsschliffen besonders deutlich hervor.

Nur sehr selten habe ich in Bildung begriffene Skulpturen gefunden, die anstelle eines Gefäßnetzes noch weite Hohlräume nach Art einer Pulpahöhle haben (Abb. 1 E, *plh*). Diese Hohlräume sind noch von weichem Pulpagewebe erfüllt gewesen, das aber sicher bereits die Gefäßkanäle enthielt, die das spätere Gefäßnetz bilden. Je jünger die Bildung ist, um so dünner sind ihre Wände, und entsprechend gering sind ihre Aussichten, erhalten zu bleiben.

Eine auffallende Bildung von *Traquairaspis* ist die dichte glatte Dentindecke im zentralen Feld der Ventralplatte. Ihr Vorhandensein veranlaßte Brotzen zu der sehr begreiflichen Aufstellung seiner Gattung *Orthaspis*. Gross (1947, S. 94) wies nach, daß *Orthaspis* — ebenso wie *Phialaspis* Wills — einen skulptierten Panzer hat, der nur im Zentrum bestimmter Platten glatt und eben wird. Diese Fläche des Ventralpanzers zeigt sehr interessante Bildungserscheinungen (Abb. 2 E—F, Abb. 5 A—F). Die Dentindecke (*dnd*) schließt die hier meist gekammerte Spongiosa (*ka.sp*) oder Mittelschicht nach oben ab, sie ruht gewissermaßen auf den senkrechten Kammerwänden der Spongiosa (Abb. 5 B), die sich aber nicht in die Dentindecke fortsetzen. Die Dentindecke ist demnach eine zusammenhängende Schicht, kein Feld polygonaler, durch Aspidinstreifen

Abb. 4. *Traquairaspis* sp. indet. Dünschliffe durch den Panzer. A Schliff Nr. 2162 Berlin; Horizontalschliff durch junge Dentinleiste mit noch weiten Kanälen; × 65. B Schliff Nr. 2160 Berlin; Horizontalschliff durch Dentinleiste mit primärem und sekundärem Dentin; × 65. C Schliff Nr. 2171 Berlin; Horizontalschliff durch oberste Lage der Dentindecke des Ventralpanzers; × 125. D Schliff Nr. 2171 Berlin; vgl. Fig. C; × 125; zeigt das Hervorgehen der Dentinröhrchen aus Pulpakanälen. E Schliff Nr. 2166 Berlin; Horizontalschliff durch Teil einer Dentinleiste mit primärem und sekundärem Dentin (Dentone); × 125. F Schliff Nr. 2598 Berlin; Vertikaler Querschliff durch Schuppe (?) mit zwei Dentinleisten-Generationen (vgl. Abb. 1 F); × 65. dn_{I-I} primäres und sekundäres Dentin; dnl_{I-II} Dentinleisten der ersten und zweiten Generation; $dnl_{II-III?}$ Sockel der Dentinleisten der zweiten und dritten Generation; *dnt* Denton; *dr* Dentinröhrchen; *msch* Mittelschicht; *plk* Pulpakanal; *plx* oberer Kanalplexus in der Dentinleiste; *usch* Unterschicht.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getrennter Dentinplättchen. Schaut man durch das Mikroskop von oben auf die recht durchsichtige Decke, so erscheinen zahlreiche feine Pünktchen ohne jede Anordnung gleichmäßig verteilt. Senkt man den Tubus, so wandeln sich die Pünktchen in feinste Ausläufer der Dentinröhrchen, die sternförmige Figuren in diffuser Anordnung bilden (Abb. 4 C, *dr*). Senkt man den Tubus noch weiter, so treten nun die Dentinröhrchen selber in Erscheinung, die auf die Querschnitte von Pulpakanälen hin konvergieren (Abb. 4 D). Zugleich werden die Wände der Spongiosakammern und Dentinfüllungen (dn_2) bzw. Aspidinfüllungen der ehemaligen Pulpahöhlen sichtbar. Ein im Querschnitt ringförmiger, sehr heller Streifen trennt die Dentinfüllung vom Aspidin der Kammerwände (Abb. 4 D). Diese Dentinfüllung ist nicht selten sehr deutlich lamellär geschichtet.

In der Abb. 2 F ist ein Teil der Spongiosawand, die aus feinlamellären Aspidin besteht, wiedergegeben. Man sieht daneben die etwas höher gelegene Dentindecke, die im Bereich der Kammerwand, auf die das Mikroskop eingestellt ist, nicht sichtbar wird. Ergänzt wird diese Abbildung durch Abb. 2 E, die einen Vertikalschliff wiedergibt. Die Dentindecke (*dnd*) ist bereits fertig ausgebildet, aber anstelle enger Pulpakanäle finden sich noch die weiten Pulpahöhlen (*ka.sp*), die den gewöhnlichen Spongiosakammern entsprechen. Aus diesen Höhlen steigen die Dentinröhrchen auf und bilden die üblichen Arkadenverbindungen (*ark*), die ebenfalls Dentinröhrchen entsenden. Beim fortschreitenden Reduktionsprozeß des Kammerhohlraumes wird die Oberhälfte der Kammer mit Dentin bzw. Aspidin erfüllt, durch welches einzelne Dentinröhrchen oder die Oberenden der Pulpakanäle nach oben streben (Abb. 5 A). Die Decke der Mittelschicht wird weiter verdickt und verfestigt. Die Dentindecke hebt sich durch das Fehlen von Sharpeyschen Fasern sehr deutlich von dem primären Aspidin ab, das meist sehr dicht von diesen Fasern erfüllt ist.

Die geschlossene Dentindecke des Mittelfeldes der Ventralplatte erinnert sehr an die massive Dentinausfüllung der Spongiosahohlräume im Ventralschild und im Rande der Branchialplatte der Psammosteida. Bei *Traquairaspis* ist der Prozeß lange nicht so weit fortgeschritten, es kommt nur zur Bildung einer relativ dünnen abschließenden Decke der Spongiosa, bei *Psammolepis* dagegen zur Aus-

Abb. 5 A—F. *Traquairaspis* sp. indet. A Schliff Nr. 474 Berlin; Vertikalschliff durch Dentindecke und sehr verengte Spongiosakammern des Mittelfeldes des Ventralpanzers; × 65. B Schliff Nr. 470 Berlin; Vertikalschliff durch junge Dentindecke des Ventralpanzers; × 65. C—F Schemata zur Veranschaulichung der Bildung und Verdickung der ventralen Dentindecke und des Spongiosa; etwa × 65. G—K *Anglaspis* sp. indet. Schuppen- und Panzerreste; × 16. G—H (f 656, 657) Teile von Schuppen mit Quer- und Längsleisten; J und K (f 658, 659) Teile des Panzers mit Mündungen der Sinneskanäle in den Dentinleisten. *asp.la* Aspidin-Lamellen; *dn.la* Dentin-Lamellen; *dnd* Dentindecke; dnd_1 oberste Lage der Dentindecke; *dnl.l* Längsleiste; *dnl.q* Querleiste; *dr* Dentinröhrchen; *k* Kante der Dentinleiste; *ka.sp* Spongiosakammer; *mla* Mittellamelle; *plk* Pulpakanal; *po.sn* Mündungspore der Sinneskanäle; *po.zwr* Poren der Zwischenrinnen; *vrd* Vorderende; *zwr* Zwischenrinne.

füllung aller Hohlräume der gesamten Spongiosa, von oben nach unten (Ventralplatte) oder von außen nach innen (Branchialplatte) fortschreitend.

Hin und wieder findet man Skulpturen, die auf Bruchflächen oder in Dünnschliffen zeigen, daß sie aus zwei Dentingenerationen bestehen (Abb. 3 B und C; Abb. 8 E). Ein innerer schmaler und niedrigerer Dentinwall (dnl_I) wird von einem wesentlich größeren (dnl_{II}) umschlossen und überlagert. Äußerlich ist von der Mehrfachbildung nichts zu sehen. Gefäßkanäle der Mittelschicht, die auf der Oberfläche zwischen den Dentinskulpturen münden, wandeln sich zu Pulpakanälen, die nach den Außenseiten und nach oben in üblicher Weise Dentinröhrchen ausstrahlen. Seitwärts von dem primären Dentinwall liegen diese zu Pulpakanälen gewordenen Gefäßkanäle ein wenig vom primären Dentin entfernt, auf das auch einige kurze Dentinröhrchen gerichtet sind (Abb. 3 C, links). Über dem primären Dentinwall bilden die seitlich aufsteigenden Pulpakanäle einen Kanalplexus, aus dem die Dentinröhrchen strahlen, die den Scheitel des sekundären Dentinwalls aufbauen. In den eben beschriebenen Fällen beobachten wir an den primären Dentinskulpturen keine Resorptionserscheinungen. Das scheinbare Hindurchtreten eines Gefäßkanals aus dem primären Dentinwall (Abb. 3 C rechts) ist durch die Bildung einer Seitenzacke (*dnl.z*) bedingt, die vor dem erwähnten Kanal liegt. Eine weiter hinten im Schliff folgende Seitenzacke des sekundären Dentinwalls ist auf der linken Seite des Schliffes zu sehen.

Eine besonders interessante und regelmäßige Mehrfachbildung der Dentinskulpturen fand ich in einem recht stark gewölbten Rest, der vielleicht einer Schuppe oder einer Seitenplatte angehört hat (Abb. 1 F; Abb. 3 D und E; Abb. 4 F). Leider ist eine ursprünglich wohl vorhanden gewesene dritte Dentinlage beim Durchschneiden des spröden Restes verlorengegangen. Wir orientieren uns an den Abb. 3 E und 4 F, die Teile des Restes in vertikalen Querschnitten zeigen. Auf die von vielen Sharpeyschen Fasern erfüllte Unterschicht (*usch*) folgt eine dünne Mittelschicht (*msch*), die eine einfache Lage breiter Blutgefäße enthält. Aus einem Teil dieser Kanäle strahlen Dentinröhrchen aus; es sind Pulpakanäle (plk_I), die sehr regelmäßig angeordnete Dentinwälle (dnl_I) aufbauen, die in recht weiten Abständen kurze Seitenzacken abgeben können (Abb. 1 F). An der Basis mancher dieser Dentinwälle sind deutlich zwei horizontal verlaufende Pulpakanäle zu erkennen (Abb. 3 E, links). Zwischen den recht dicht angeordneten Dentinwällen erheben sich aus der Mittelschicht senkrecht oder schräg nach oben aufsteigende Blutgefäßkanäle, die nach beiden Seiten über die Dentinwälle der ersten Generation horizontale Pulpakanäle (plk_{II}) abgeben, die die Dentinwälle der zweiten Generation aufbauen.

Die Dentinwälle der zweiten Generation (dnl_{II}) sind breiter und höher als die der ersten Generation, sie überdecken daher gelegentlich auch zwei Dentinwälle der ersten Generation (Abb. 3 E, rechts). Zwischen den Dentinwällen der zweiten Generation, die in der Abb. 1 F von oben zu sehen sind, setzen sich die aufsteigenden Blutgefäßkanäle fort. Ihr Verlauf ist recht unregelmäßig, zwischen ihnen

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findet sich bereits ein tertiäres, weißlich trübes Dentin (dnl_{III}), das allem Anschein nach die basalen Teile der Flanken einer dritten Generation von Dentinwällen bildete. Die Dentinwälle der zweiten Generation sind nicht anders aufgebaut als die der ersten Generation. Auch an ihrer Basis verlaufen meist zwei horizontale Pulpakanäle, aus denen die Dentinröhrchen und senkrechte Pulpakanäle bzw. Dentinröhrchenbündel aufsteigen. Aber die horizontalen Kanäle entsenden auch spärlich Dentinröhrchen nach unten (Abb. 3 E). Der Dentinwall der zweiten Generation umfaßt den der ersten mit einem breiten Sockel (*dnl.s*), der im Querschnittsbild den primären Dentinwall als seitliche Zunge begleitet. Die vermutete dritte Dentingeneration hat anscheinend unregelmäßig angeordnete Dentinskulpturen gebildet.

Die Flanken der Dentinwälle sind spiegelglatt und zeigen oft deutlich die schmale Grenzfurche, die für die Skulpturen von *Traquairaspis* so charakteristisch sind (Abb. 1 F, links). Die fast ebenen Oberflächen der Dentinwälle beider Generationen sind dagegen etwas rauh und trüb, wie angeätzt. Schliffe aller Ebenen zeigen nun sehr deutlich, daß nicht nur die senkrecht aufsteigenden Dentinröhrchen, sondern sogar die engen aufsteigenden Pulpakanäle bzw. Dentinröhrchenbündel die Oberfläche der Dentinwälle erreichen (Abb. 3 E; Abb. 4 F) und hier als offene feine Poren erscheinen. Es hat also Resorption stattgefunden, ehe die zweite bzw. dritte Dentingeneration abgelagert wurde. Daher sind auch die Dentinwälle oben abgeplattet und nicht wallartig gewölbt, wie sonst alle Skulpturen bei *Traquairaspis* (vgl. Abb. 3 B und E). Nach Beendigung der Resorption legte sich über die vorher gebildeten Dentinwälle das neue Dentin der folgenden Generation. Die Resorption ist so weit gegangen, daß sie vielfach die arkadenförmigen Verbindungen der Pulpakanäle abgeschnitten hat. Die Resorption erklärt auch die rauhe Oberflächenbeschaffenheit der Dentinwälle. Mehrfachbildung von Dentinskulpturen sind bei Heterostraci sehr selten, sie finden sich nur bei Psammosteiden recht häufig (Gross 1930 und 1933, Bystrow 1955, Stensiö 1957 und Ørvig, im Druck). Noch seltener sind bei Heterostraci Resorptionserscheinungen. Besonders auffallend ist bei *Traquairaspis* die Regelmäßigkeit der Bildung mehrerer Dentingenerationen von Skulpturen genau übereinander.

Maße. Die oberen Dentinwälle sind 160 μ hoch, die unteren etwa 120—145 μ. Die oberen Skulpturen sind 420—480 μ breit, die unteren 240—270 μ.

Die Mittelschicht (Abb. 2 C—G; Abb. 3 A, Abb. 8 E). Die Mittelschicht liegt in zwei durch schrittweise Übergänge verbundenen Ausbildungen vor, als retikuläre oder cancelläre Spongiosa. In den dicken Randpartien der Platten findet sich bevorzugt die reticuläre Spongiosa (Abb. 2 D und 3 A); engere Blutgefäßkanäle erfüllen die Schicht in vielfachen Lagen und unregelmäßiger Anordnung. Die Kanäle münden auf der Oberfläche der Mittelschicht zwischen den Dentinskulpturen (Abb. 1). Sie erheben sich in die Basis der Dentinwälle und bilden dort den Gefäßplexus, der die Pulpakanäle abgibt (Abb. 2 A—D). Weite Teile der großen Platten sind dagegen von einer cancellären, weitkam-

merigen Spongiosa erfüllt (Abb. 2 C, E; Abb. 5 B; Abb. 8 E). Die großen Kammern sind sehr regelmäßig angeordnet, meist bilden die Kammern nur eine Lage. Die Kammerwände sind dünn (Abb. 5 B) und werden nur von wenigen engen Poren durchbohrt (Abb. 2 C), die die Verbindungen zu den Nachbarkammern herstellen. Über der cancellären Spongiosa kann sich manchmal eine dünne Lage retikulärer Spongiosa entwickeln (Abb. 2 C).

Die Mittelschicht besteht aus Aspidin, das meist von zahlreichen Sharpeyschen Fasern erfüllt ist (Abb. 3 A). Die Fasern verlaufen oft in Zügen und Bündeln ganz verschiedener Richtung. In den Kammerwänden sind sie hingegen meist recht genau radial gerichtet (Abb. 2 C, E und F; Abb. 5 A). Gehen sie von Hohlräumen aus, so können sie bis zu einem gewissen Grade Dentinröhrchen vortäuschen. Am Fehlen der Sharpeyschen Fasern kann man oft sehr schön das sekundäre, nachträglich um die Gefäßkanäle oder als Ausfüllung der Spongiosakammern entstandene Dentin bezw. Aspidin erkennen. Es bildet sehr deutlich lamellierte Röhren oder Körper, die unmittelbar mit den primären Osteonen des Knochengewebes zu vergleichen sind. Knochen, Dentin und Aspidin bilden die gleichen lamellierten Röhren, die man als primäre Osteone, Dentone und Aspidone bezeichnen kann, Ausfüllungen ehemaliger Hohlräume (Abb. 4 B, D, E), weiter Gefäßkanäle oder Spongiosakammern. Die feinen Lamellen dieses sekundären Aspidins gehen an der Grenze zum Dentin kontinuierlich in dieses über.

In der oberen Hälfte der Spongiosa liegen auch die weiten Kanäle der Sinneslinien (Abb. 2 C). Sie stehen mit zahlreichen Gefäßkanälen der Spongiosa in Verbindung. Ihre Zweigkanäle, die schräg aufsteigen und auf der Oberfläche der Platten zwischen den Skulpturen münden, behalten den Durchmesser der Sinneskanäle in der Spongiosa.

Die Unterschicht (Abb. 2 G; 3 A) besteht aus Aspidin, das seinen feinlamellierten Bau nur dann zeigt, wenn Sharpeysche Fasern fehlen oder spärlich sind. Die Feinfasern dieser Lamellen sind nicht regelmäßig angeordnet, so daß es nicht zur Bildung sich in den Lagen regelmäßig überkreuzender Faserzüge kommt. Unter gekreuzten Polars sieht man daher auch nicht abwechselnd dunkle und helle Streifen wie im Isopedin der Cephalaspida, Rhipidistia und Dipteriden. Die Unterschicht wird selten von aufsteigenden Kanälen durchbrochen, die das Kanalnetz der Mittelschicht versorgen; ihnen fehlen — wie allen Heterostraci — primäre Osteone bzw. Aspidone. Die Unterschicht geht ohne histologische Grenze in die Mittelschicht über, deren Beginn durch die Spongiosakammern oder Spongiosakanäle angezeigt wird. Im allgemeinen ist auch die Unterschicht von sehr zahlreichen Sharpeyschen Fasern in jeder nur denkbaren Richtung erfüllt.

ANGLASPIS SP. INDET.

Überraschenderweise fanden sich in dem bereits erwähnten Geschiebe Bey. 37 recht zahlreich kleine Panzerbruchstücke und Schuppenreste der Gattung *Ang-*

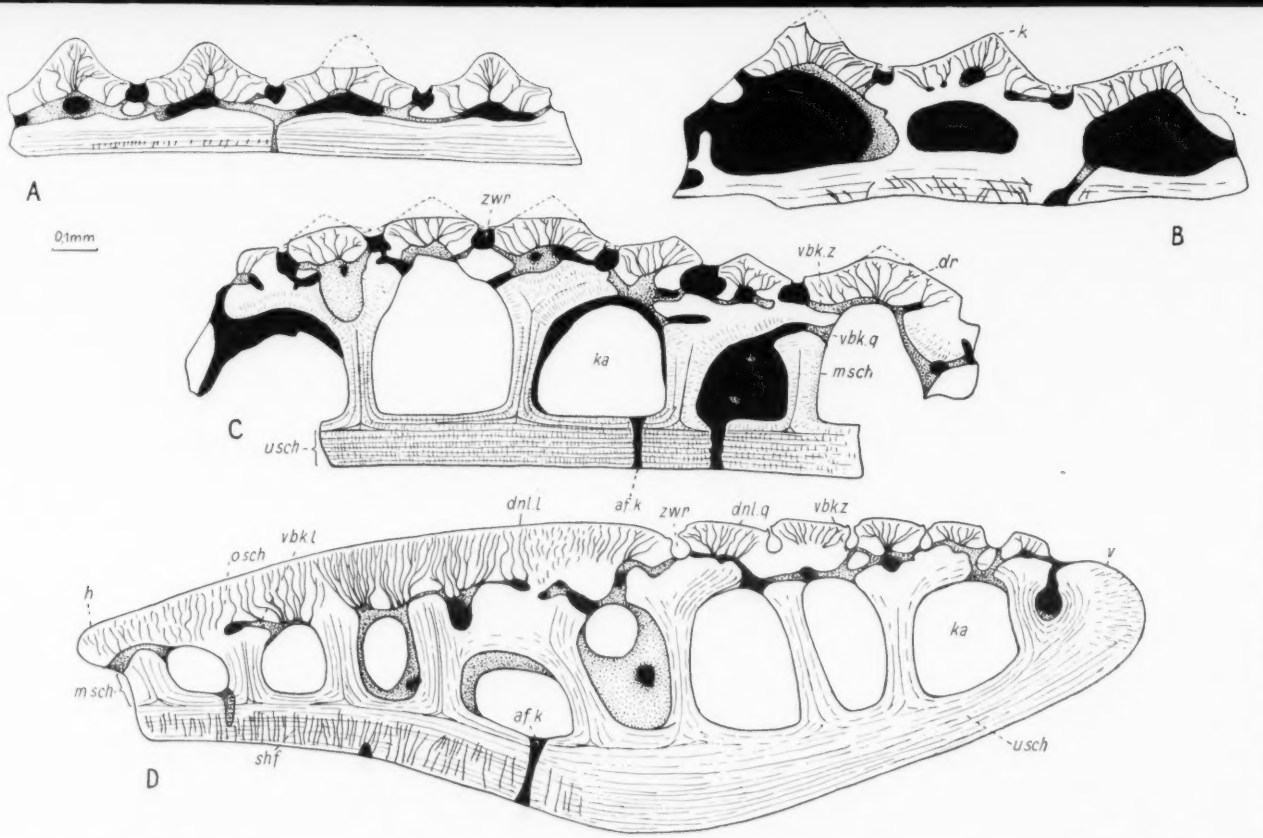
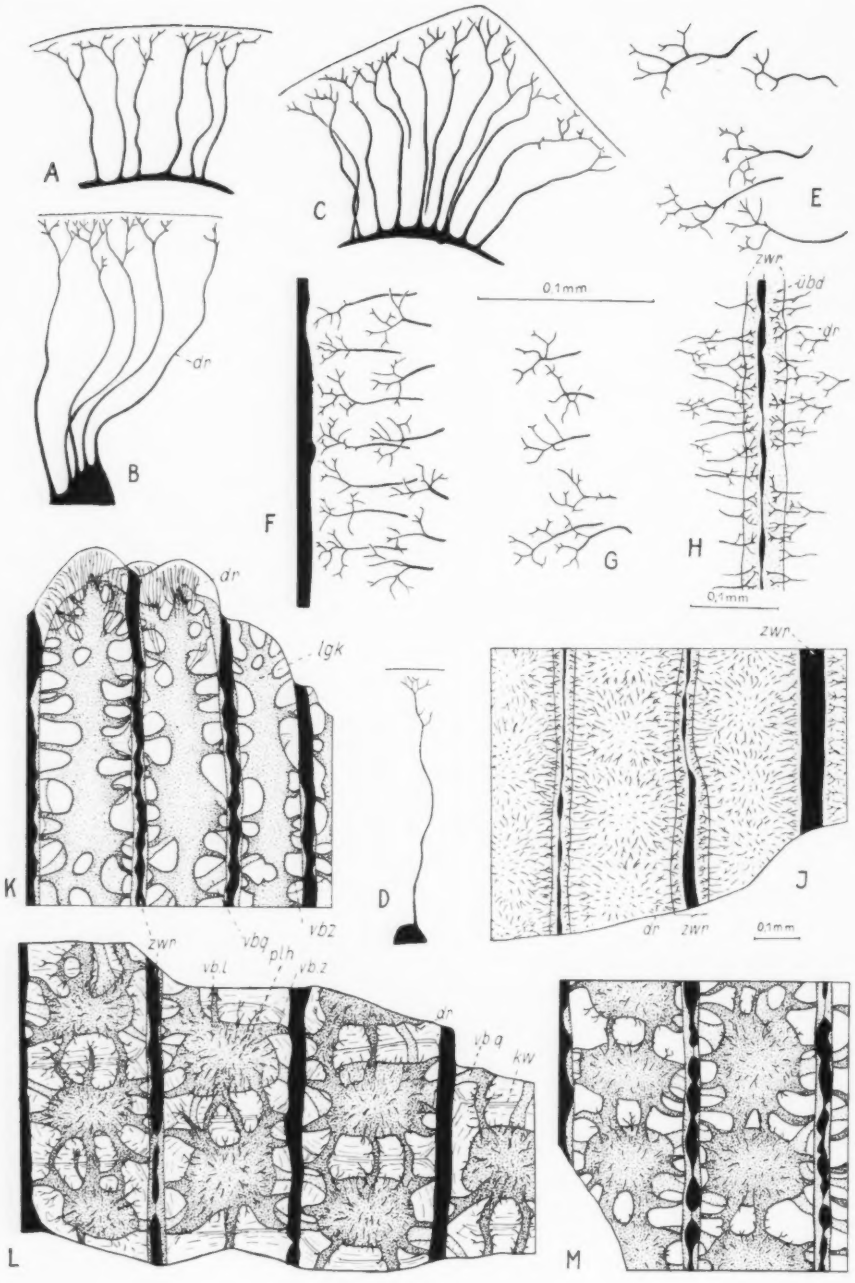


Abb. 6. *Anglaspis* sp. indet. Vertikalschliffe; × 65. A Schliff Nr. 2173 Berlin; vertikaler Querschliff durch sehr dünnen Rest. B Schliff Nr. 2174 Berlin; vertikaler Querschliff durch Rest mit noch weiten Pulpahöhlen bzw. Spongiosakammern. C Schliff Nr. 2178 Berlin; vertikaler Querschliff durch Schuppe mit weiten Spongiosakammern. D Schliff Nr. 2180 Berlin; vertikaler Längsschliff durch eine Schuppe, deren Querleisten (rechts) quergetroffen sind. *af.k* aufsteigender Kanal der Unterschicht; *dnl.l* Längsleiste; *dnl.q* Querleiste; *dr* Dentinröhrchen; *h* Hinterende der Schuppe; *k* Kante der Dentinleiste; *ka* Spongiosakammer; *msch* Mittelschicht; *osch* Oberschicht; *usch* Unterschicht; *v* Vorderende der Schuppe; *vbk.l* Verbindungskanal zwischen den Kammern unter einer Leiste; *vbk.q* Verbindungskanal zu den Kammern der Nachbarleiste; *vbk.z* Verbindungskanal zur Zwischenrinne; *zwr* Zwischenrinne.


A
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laspis Kiaer, deren Skulptur, Sinneskanalporen und Histologie weitgehend den Beobachtungen Bystrows (1955) an *Anglaspis macculoughi* Woodw. entsprechen. Die Bruchstücke reichen für eine Bestimmung der Spezies jedoch nicht aus.

Die Reste (Abb. 5 G—K) sind recht zart, da die Spongiosa fast immer cancellär entwickelt ist. Besonders charakteristisch ist, daß alle Dentinleisten der Oberschicht einen deutlichen Kiel (*k*) haben und wie hochpoliert glänzen. Am Vorderende der Schuppen finden sich meistens querverlaufende Dentinleisten (*dnl.q*), die rechtwinklig zu den Längsleisten (*dnl.l*) gerichtet sind (Abb. 5 G und H; Abb. 6 D, rechts), seltener bilden die vorderen Leisten einen Bogen oder sind bogenförmige Fortsetzungen randlicher Längsleisten. An diesem Merkmal der Leistenanordnung sind die Schuppen von *Anglaspis* leicht zu erkennen.

Die Dentinleisten bilden die dünne Oberschicht, die Mittelschicht ist meist als großkammerige Spongiosa entwickelt, die Unterschicht ist ausgeprägt und verhältnismäßig dick.

Die Dentinleisten sind recht zart und bedecken oft unmittelbar die großen Kammern der Spongiosa. An den Seitenrändern sind sie ein wenig abgeflacht (Abb. 5 H) und stets fein gezackt. Die Zacken benachbarter Dentinleisten können alternieren oder stehen sich gegenüber, wobei es sehr oft zur Berührung der Zacken kommt (Abb. 5 J und K). Zwischen den Dentinleisten bilden sich die für die Pteraspida und viele Cyathaspida typischen Rinnen (*zwr*), die zwischen den Querverbindungen der benachbarten Leisten mit einer Reihe feiner längsovaler Poren (*po.zwr*) münden. Oft berühren sich die benachbarten Leisten mit ihren Randsäumen auf größere Erstreckung, so daß die Rinnen geschlossen werden (Abb. 5 G). Der Querschnitt der Rinnen ist niedrig, etwa kreisförmig (Abb. 6). Da die dünnen Randsäume meist abgebrochen sind, stehen die Rinnen oft weit offen (Abb. 7 J).

Die Querleisten am Vorderende der Schuppen (Abb. 5 G und H; Abb. 6 D) sind schmaler als die Längsleisten und greifen von vorne nach hinten vielfach ein wenig übereinander, so daß die Rinnen von oben kaum zu sehen sind. Nach

Abb. 7. *Anglaspis* sp. indet. Dünnschliffe durch die Oberschicht. A—D Dentinröhrchen im Vertikalschliff; × 255. E—G Dentinröhrchen im Horizontalschliff, seitlich von den Zwischenrinnen; × 255. H Horizontalschliff durch Zwischenrinnenmündung mit angrenzenden Dentinröhrchen; das Dentindach über der Zwischenrinne punktiert; × 125. A Schliff Nr. 2633 Berlin; B Schliff Nr. 2180 Berlin; C Schliff Nr. 2636 Berlin; D Schliff Nr. 2180 Berlin; E Schliff Nr. 2184 Berlin; F Schliff Nr. 2634 Berlin; G Schliff Nr. 2184 Berlin; H Schliff Nr. 2634 Berlin; J Schliff Nr. 2634 Berlin; Horizontalschliff durch Dentinleisten, hocheingestellt; × 65. K Schliff Nr. 2182 Berlin; Horizontalschliff durch Dentinleisten, tiefer eingestellt; zeigt durchgehende Längskanäle; × 65. L Schliff Nr. 2183 Berlin; Horizontalschliff durch Dentinleisten mit getrennten Spongioskammern; × 65. M Schliff Nr. 2184 Berlin; Horizontalschliff durch Dentinleisten mit Spongiosakammern; × 65. *dr* Dentinröhrchen; *kw* Kammerwände; *lgk* Längskanal unter der Dentinleiste; *plh* Pulpahöhle; *plk* Pulpakanal; *übd* Überdachung der Zwischenrinne; *vb.l* Verbindungskanal zwischen den Kammern unter einer Leiste, strahlt Dentinröhrchen aus; *vb.q* Verbindungskanal zur Kammer der Nachbarleiste, ohne Dentinröhrchen; *vb.z* Verbindungskanal zur Zwischenrinne, ohne Dentinröhrchen; *zwr* Zwischenrinne.

vorne werden die Querleisten zunehmend schmaler; vor ihnen ist das Vorderende (*vrd*) der Schuppen frei von Skulpturen.

Bei Leistenvermehrung schalten sich meist neue Leisten zwischen die vorhandenen, seltener sind Leistenabspaltungen (Abb. 5 J und K). Vielfach findet man die Mündungsporen der Sinneslinien (*po.sn*), die immer im Bereich der Leisten liegen, entweder inmitten des einfachen oder schlingenförmigen Endes der Leiste oder etwas seitwärts in der Leiste, so daß ein Rand der Sinnespore an die Zwischenrinne grenzt. Das geringe Material erlaubt nicht, alle Möglichkeiten der Porenmündungen kennen zu lernen. Die Tubuli der Sinneslinien steigen ziemlich steil nach oben, so daß die Ränder der Poren überall scharf sind.

Maße. Die Breite der Längsleisten der Schuppen schwankt zwischen 200 bis 325 μ, die der Querleisten zwischen 75 und 200 μ. Die Höhe der Dentinleisten kann 125 μ betragen. Der Durchmesser des Sinnesporen erreicht 75 bis 125 μ. Die Breite der Zwischenrinnen kann 25—105 μ betragen, aber sich auch bis zum Verschluß verengen. Die Poren der Zwischenrinnen sind 25 bis 75 μ lang.

Histologie (Abb. 6 und 7). Auch histologisch sind die vorzüglich erhaltenen Reste meist leicht zu erkennen, die Dentinröhrchen und vielfach auch die Spongiosakammern haben eine charakteristische Gestalt. Die skulptierte Oberschicht ist am dünnsten, die Mittelschicht ist meistens am stärksten entwickelt, aber auch die Unterschicht ist oft auffallend dick (Abb. 6 C und D).

Die Dentinleisten bedecken oft unmittelbar als Dach die Spongiosakammern, nicht selten sind sie aber auch von ihnen durch eine dünne, von Gefäßkanälen erfüllte Aspidinschicht getrennt. Die Dentinröhrchen strahlen dementsprechend einfach aus den Spongiosakammern oder aus Pulpakanälen, die sich zwischen den Kammern oder über ihnen entwickeln. Die Dentinröhrchen haben einen recht unregelmäßig geschlängelten Verlauf (Abb. 7 A—D); sie verästeln sich wurzelförmig dicht unter der Oberfläche der Dentinleisten. Es kommt nicht zu der Bildung wohlunterscheidbarer Dentinschichten. Schaut man durch das Mikroskop auf die Dentinleisten, so erscheinen die Enden der Dentinröhrchen zuerst im Grat der Leiste, dann auf den schräg abfallenden Seitenflächen und zuletzt in den Seitenrändern (Abb. 7 E—H). Selbst wenn die Seitenränder benachbarter Dentinleisten sich auf weite Strecken berühren, so verbinden sich die Ausläufer der Dentinröhrchen benachbarter Leisten niemals (Abb. 7 J). Besonders lange Dentinröhrchen strahlen aus den Enden der Leisten (Abb. 7 K). Das Dentin von *Anglaspis* ist verhältnismäßig weniger dicht von Dentinröhrchen erfüllt als bei den anderen Heterostraci-Gattungen.

Ein besonderes Interesse beanspruchen die dentinbildenden Pulpakanäle und die Spongiosakammern, deren Oberhälfte eine Art Pulpahöhle bildet. Ganz dünne Reste (Abb. 6 A) bestehen aus einer dickeren Unterschicht, einer einzigen Lage von horizontal ausgebreiteten Gefäßkanälen, die die Spongiosa bilden, aber zugleich auch als Pulpakanäle der Oberschicht dienen, da sie in ihrer ganzen Ausdehnung nach oben Dentinröhrchen ausstrahlen und die Zwischenrinnen mit

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engen Gefäßkanälen versorgen. Sehr häufig aber strahlen die Dentinröhrchen unmittelbar aus den Spongiosakammern und ihren oberen Verbindungskanälen (Abb. 6 B—D; Abb. 7 J—M). In Horizontalschliffen kann man die Verhältnisse besonders gut übersehen. Abb. 7 K zeigt einen Rest, bei dem unter den Dentinleisten ein unregelmäßig gestalteter und verschieden breiter Längskanal (*lgk*) verläuft, der zahlreiche enge schräg aufsteigende Querkanäle (*vb.z*) an die Zwischenrinnen (*zwr*) abgibt. Die Querverbindungen zu den Längskanälen der Nachbarleisten (*vb.q*) liegen viel tiefer und unterführen die Zwischenrinnen (heller punktierte Kanäle). Der abgebildete Rest weist nur gering entwickelte Zwischenwände und Kammerbildungen auf.

Sehr ausgeprägt ist die Kammerbildung in den Resten, die in den Abbildungen 7 L und M wiedergegeben sind. Man erkennt deutlich die Wände zwischen den Kammern (*kw*), auf die sich nachträglich viel Aspidin aufgeschichtet hat, welches das Lumen der Kammern verringert. Die Kammern liegen streng in der Längsrichtung der Leisten angeordnet, was bei anderen Stücken oft nicht der Fall ist und einer völligen Unregelmäßigkeit der Kammern im Verhältnis zu den Skulpturen weicht. Die Kammern haben eine querovale bis querrechteckige Gestalt; ihre Vorder- und Hinterwände sind lang, die Querwände sind relativ kurz. In der Längserstreckung der Leisten sind sie durch recht zahlreiche enge, nach oben gewölbte Kanäle verbunden (*vb.l*), aus denen in gleicher Weise wie aus der Decke der Spongiosakammern die Dentinröhrchen ausstrahlen. Sie gleichen den Arkadenkanälen anderer Gattungen. An den kurzen Querenden verbinden sich die Spongiosakammern durch enge Kanäle (*vb.z*) mit den Zwischenrinnen (vgl. auch Abb. 6). Die Verbindungen zu den Spongiosakammern der Nachbarleisten werden durch jeweils einen oder zwei breitere Kanäle (*vb.q*) hergestellt, die viel tiefer liegen, unterhalb der Zwischenrinnen. Diese Kanäle geben ebenso wenig Dentinröhrchen ab wie die Verbindungskanälchen zu den Zwischenrinnen. In hoher Aufsicht (Abb. 7 J) erkennt man schon aus der Anordnung der Dentinröhrchen-Querschnitte die Anordnung und Ausdehnung der Spongiosakammern. Die Spongiosakammern der abgebildeten Schliffe sind tief braunrot gefärbt und ähneln in der Aufsicht (Abb. 7 L und M) fast an eine Reihe breiter Milben mit kurzen Beinen.

Die Mittelschicht wird meist durch eine Lage großer Spongiosakammern gebildet. Oft sind die Wände der Kammern auffallend dick, die Verbindungskanäle zu Nachbarkammern sind eng (Abb. 6 C und D). Der lamelläre Bau des Aspidins und seine feine radiale Faserung treten meist sehr deutlich in Erscheinung, da sich in den von mir untersuchten Resten viel weniger Sharpeysche Fasern finden als bei *Traquairaspis* und anderen Heterostraci.

Sehr deutlich lamelliert ist auch die verhältnismäßig dicke Unterschicht (Abb. 6), die nur von sehr wenigen Gefäßkanälen (*af.k*) senkrecht durchbohrt wird. Diese Kanäle umwanden sich wie bei allen Heterostraci nicht mit Aspidinlamellen, bilden also keine Aspidone. Die obersten Lamellen der Unterschicht

bilden den Boden der Spongiosakammern (Abb. 6 C), so wie deren Decken meist von der Oberschicht, dem Dentin, geliefert werden.

Die geringe Anzahl der Reste genügt nicht, um alle Erscheinungsformen im strukturellen Aufbau des Panzers kennenzulernen. Bilder, wie sie Bystrow (1955, Fig. 14 und 15) in leichter Schematisierung gegeben hat, finden sich oft, doch sind sie nicht die einzigen Möglichkeiten.

M a ß e. Die Dentinröhrchen sind meist 90 bis 120 μ lang. Die Dentinleisten sind etwa 125 μ hoch. Die Zwischerinnen könnes bis 105 μ breit und 42 bis 60 μ tief werden. Die von den Spongiosahohlräumen zu den Zwischenrinnen führenden Verbindungskanäle sind nur 6 bis 12 μ dick, ein etwas größeres Kaliber haben die Verbindungskanäle zwischen den Spongiosakammern einer Dentinleiste, nämlich 25 bis 45 μ. Die Verbindungskanäle zu den Kammern unter der Nachbarleiste können dagegen eine Breite von 80 μ erreichen. Sehr eng (18 μ) sind die Kanäle, die die Unterschicht durchbohren. Die unter den Dentinleisten längsverlaufenden Pulpakanäle schwanken in der Breite zwischen 30 bis 180 μ.

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CORVASPIS SP. INDET.

Von dieser Gattung habe ich nur einige wenige Schuppen im Geschiebe Bey. 37 gefunden, die den Schuppen von *Corvaspis kingi* Woodw., die Dineley 1953 (Abb. 10—12; Taf. 1 Fig. 4 und 5) abbildete, völlig gleichen. *Corvaspis*-Schuppen aus dem *Psammosteus*-Limestone von Shropshire (Downton), die ich Herrn Dr. Ørvig verdanke, gleichen den Schuppen aus dem Geschiebe bis in alle Einzelheiten. Die Bestimmung der Art kann auf Grund der wenigen Schuppen nicht durchgeführt werden.

Die S c h u p p e n (Abb. 8) haben eine sehr dicke Basis, die vorne halbkreisförmig endet, hinten dagegen zugespitzt. Einige wenige Gefäßkanäle durchbohren die Unterfläche (Abb. 8 B). Die Dentinleisten der Oberschicht bilden ein rhombisches Feld, vor dem der Vorderrand der Schuppe, der von den vorausgehenden Schuppen überlagert wurde, weit hervorragt (Abb. 8 A). Die Hinterhälfte der Schuppen wird von den Dentinleisten völlig bedeckt, seitlich und am Hinterende ragt das Dentin oft ein wenig über die Basis heraus. Das Vorderende der Basis ist keulenförmig angeschwollen (Abb. 8 C, *vrd*), ein Merkmal dieser Gattung. Auf der vorderen freien Fläche der Schuppe münden zahlreiche Gefäßkanäle (Abb. 8 A).

Die Dentinleisten liegen dicht nebeneinander, in der Mitte der Schuppe die breitesten und längsten. Die seitlichen Leisten sind ein wenig nach außen gebogen, ihre Hinterenden sind abgeschrägt und zugespitzt. Vorne finden sich meist einige kurze unregelmäßig geformte Leisten, die sich oft zwischen die Spitzen der Längsleisten einschieben. Querleisten nach Art der *Anglaspis*-Schuppen fehlen. Auch vorne enden die Längsleisten zugespitzt (Abb. 8 D). Die Dentinleisten haben feine Seitenzacken, die recht deutlich schräg nach vorne gerichtet sind. Die Rinnen (*zwr*) zwischen den Leisten sind sehr schmal.

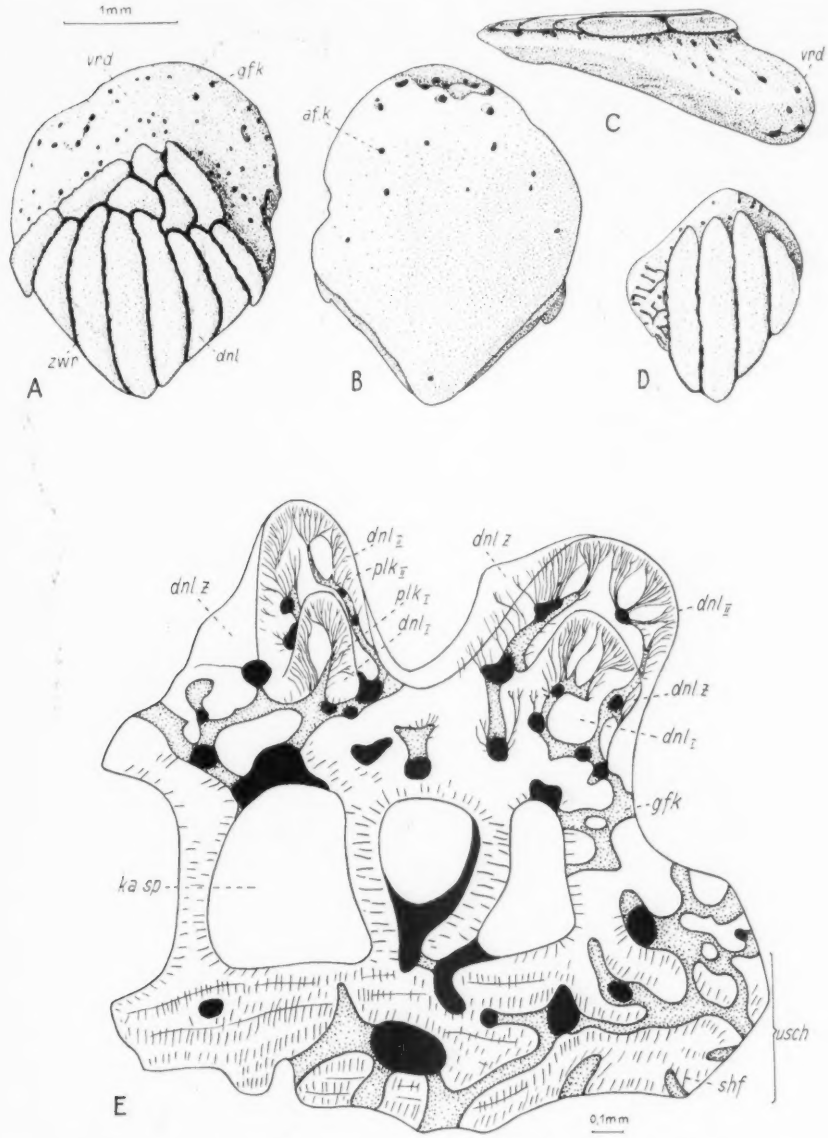
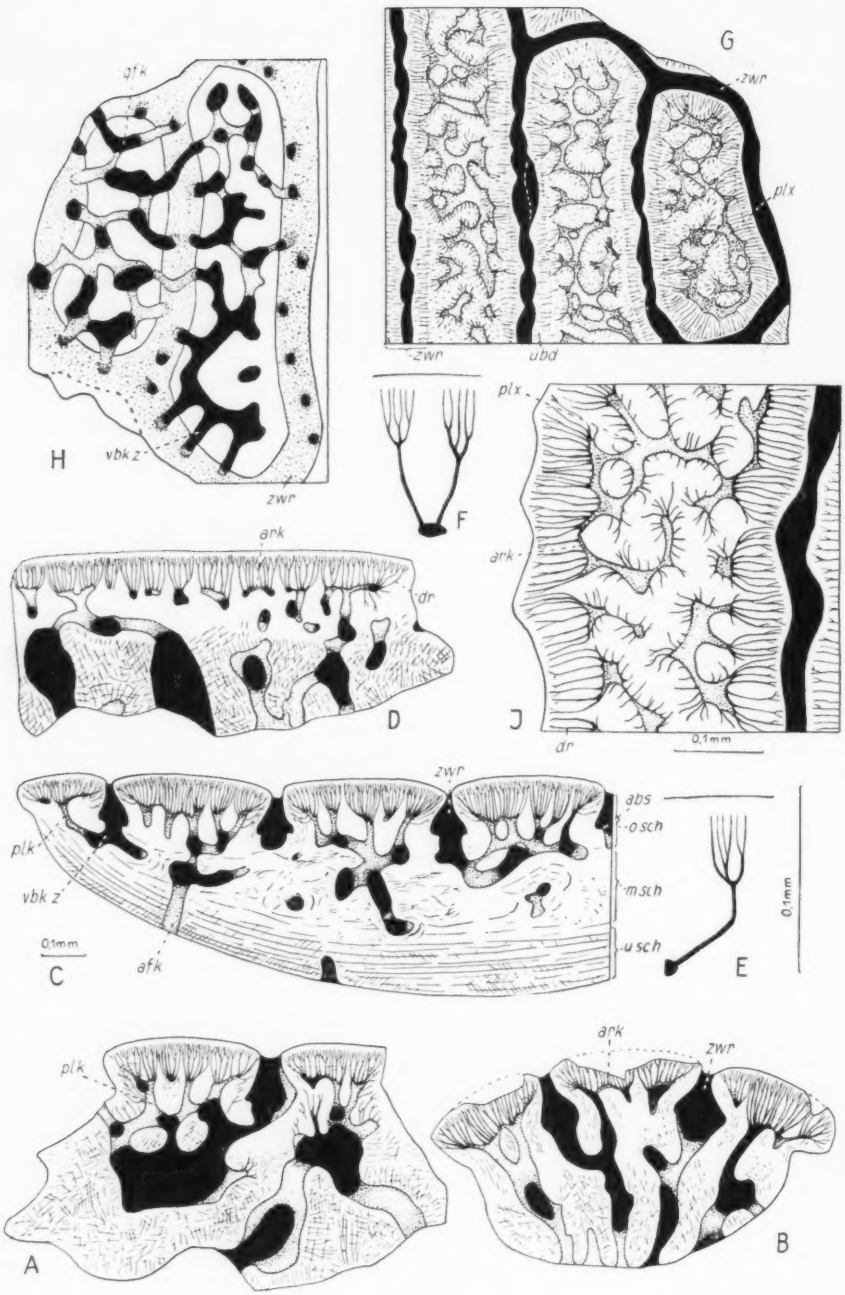


Abb. 8 A—D. *Corvaspis* sp. indet. Schuppen; × 16. A—C Schuppe von oben, unten und von der Seite; f 660. D kleine Schuppe, links eine Leiste abgelöst; f 661. E *Traquairaspis* sp. indet. Schliff Nr. 2628 Berlin; vertikaler Querschliff durch Bruchstück mit zwei Dentinleisten-Generationen (vergl. Abb. 3 B u. C); × 40. *af.k* aufsteigender Kanal; *dnl* Dentinleiste; *dnl$_{I-II}$* Dentinleisten der ersten und zweiten Generation; *dnl.z* Seitenzacke der Dentinleiste; *gfk* Gefäßkanal; *ka.sp* Spongiosakammer; *plk$_{I-II}$* Pulpakanal; *shf* Sharpeysche Fasern; *usch* Unterschicht; *vrd* Vorderende; *zwr* Zwischenrinne.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Histologie (Abb. 9). Alle abgebildeten Schliffe stammen von Schuppen; Panzerreste standen mir nicht zur Verfügung. Der histologische Aufbau der Dentinleisten dürfte im Panzer und in den Schuppen der gleiche sein. Die Unterschicht ist gegenüber der Mittelschicht wenig ausgeprägt. Beide Schichten sind überreichlich erfüllt von Sharpeyschen Fasern, die meist schräg oder horizontal in allen Richtungen verlaufen und bis in den Sockel der Dentinleisten hineinreichen können, wo sie oft eine fast senkrechte Stellung einnehmen. Auffallenderweise treten Büschel von Sharpeyschen Fasern manchmal aus den senkrecht die Unterschicht durchbohrenden Gefäßkanälen, so daß sie Dentinröhrchen entfernt ähnlich sehen können und die Ränder der Gefäßkanäle im Schliffbild auszacken.

Die Dentinleisten haben meist sehr regelmäßig angeordnete Dentinröhrchen, die aus mehr oder weniger senkrecht aufsteigenden Pulpakanälen ausstrahlen (Abb. 9 B). Die Pulpakanäle sind oft durch Arkadenkanäle verbunden, die ebenfalls Dentinröhrchen aussenden (Abb. 9 C und D). Die parallel verlaufenden Dentinröhrchen verzweigen sich alle auf gleicher Höhe (Abb. 9 A—D), so daß sich im Dentin gewisse Zonen unterscheiden lassen. Am hellsten ist die oberste Zone mit den Endbüscheln der Dentinröhrchen (Abb. 9 E—F).

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Von dem Kanalnetz der Mittelschicht gehen Kanäle aus, die fast senkrecht von unten in die Zwischenrinnen (*zwr*) münden (Abb. 9 A—C). Die Rinnen öffnen sich zwischen den Randzacken der Dentinleisten mit schmalen Spalten (Abb. 9 G). Das Fehlen von engen, hoch und seitlich mündenden Verbindungskanälen zwischen den Pulpakanälen und den Rinnen ist ein charakteristisches Merkmal für *Corvaspis*. — Das Dentin ist sehr deutlich lamelliert. Die feinen Lamellen können bis an die Endbüschel der Dentinröhrchen reichen und die Arkadenkanäle konzentrisch umgeben. Sie gehen unterhalb der Dentinröhrchen kontinuierlich in die Lamellen des Aspidins über (Abb. 9 B). Die Pulpakanäle der Dentinleisten verbinden sich untereinander durch die Arkadenkanäle, so daß ein horizontaler Plexus in der Oberhälfte der Dentinleiste entsteht (Abb. 9 G und J). Ein gröberes Netz bilden die Pulpakanäle an der Basis der Dentinleisten (Abb. 9 H). Die Abb. 9 G und H geben den gleichen Schliff wieder, einmal von oben (Abb. 9 G) und einmal von unten (Abb. 9 H) betrachtet; dabei tritt deutlich

Abb. 9. *Corvaspis* sp. indet. Dünnschliffe durch Schuppen. A Schliff Nr. 2186 Berlin; vertikaler Querschliff × 65. B Schliff Nr. 2185 Berlin; vertikaler Querschliff; × 65. C Schliff Nr. 2637 Berlin; vertikaler Querschliff × 65. D Schliff Nr. 2187 Berlin; vertikaler Längsschliff; × 65. E und F Schliff Nr. 2186; Dentinröhrchen; × 255. G Schliff Nr. 2189 Berlin; Horizontalschliff durch die Dentinleisten; × 65. H Schliff Nr. 2189 Berlin; Horizontalschliff durch die Dentinleisten, von unten betrachtet; der gleiche Schliff wie in Fig. G; × 65. J Schliff Nr. 2189 Berlin; vergrößerter Ausschnitt aus nicht abgebildetem Teil des Schliffes 2189; oberer Plexus mit Dentinröhrchen; × 125. *abs* Absatz in der Zwischenrinne; *afk* aufsteigender Gefäßkanal; *ark* Arkadenkanal; *dr* Dentinröhrchen; *gfk* Gefäßkanal; *msch* Mittelschicht; *osch* Oberschicht; *plk* Pulpakanal; *plx* Plexus der Arkadenkanäle; *übd* überdachter Teil der Zwischenrinne; *usch* Unterschicht; *vbk.z* Verbindungskanal zur Zwischenrinne; *zwr* Zwischenrinne.

hervor, wie sehr sich die Zwischenrinnen oben verengen, während die Dentinleisten gerade umgekehrt unten schmaler als oben sind.

M a ß e. Die Dentinleisten sind 200 bis 350 μ breit und 2 bis 3 mm lang. Die Zwischenrinnen sind am Absatz bis 130 μ breit, an der Mündung 10 bis 25 μ. Die Pulpakanäle haben einen Durchmesser von 25 bis 40 μ.

ONISCOLEPIS SP. INDET.

Unter den Namen *Oniscolepis* und *Strosipherus* beschrieb PANDER (1856) kleine Schuppen- und Tessera-Reste oder größere isolierte Dentinleisten. *Strosipherus* stammte von Leo an der Westküste Oesels, während die typischen *Oniscolepis*-Reste am bekannten Ohesaare-Pank gesammelt worden waren. *Strosipherus* ist äußerlich weniger gut erhalten, läßt dafür aber die mikroskopische Struktur (Pander, Tab 4 Fig. 8) gut erkennen. Sehr typisch ist das als *Oniscolepis* beschriebene Material aus dem Ohesaare-Pank (Pander, Tag. 6 Fig. 33 und 34), das man jederzeit ohne viele Mühe mit Essigsäure aus dem Gestein des Bone Beds der Fundstelle wiedergewinnen kann. Am häufigsten findet sich dort die von Pander als *Oniscolepis dentata* (Fig. 33) bezeichnete Form. Das Material vom Ohesaare-Pank ist meist sehr dunkel gefärbt und eignet sich nur relativ selten zur mikroskopischen Untersuchung. Pander gelang es nicht, von *Oniscolepis* brauchbare Dünnschliffe herzustellen, so konnte er nicht erkennen, daß *Strosipherus* und *Oniscolepis* die gleiche mikroskopische Struktur haben. Bereits ROHON (1893) stellte beide Gattungen zusammen.

Reste, die sich nicht von *Oniscolepis* und *Strosipherus* unterscheiden, finden sich nicht selten im Beyrichienkalk, sowohl in den Schichten mit *Thelodus parvidens* als auch in denen mit *Thelodus* cf. *scoticus*. Sie fehlen aber gänzlich in den roten sandigen Kalken der Geschiebe Bey. 36 und 37, die reichlich Bruchstücke von *Traquairaspis* und den anderen in dieser Arbeit beschriebenen Ostracodermen führen. 1947 hatte ich die Reste aus dem Beyrichienkalk — Pander folgend — teils als *Strosipherus,* teils als *Oniscolepis* beschrieben. Die sehr großen, gewölbten, isolierten Dentinleisten bezeichnete ich als *Stosipherus,* die kleinen Reste mit zierlichen Dentinleisten dagegen als *Oniscolepis.*

Dr. Ørvig verdanke ich etwas Gestein aus dem Ohesaare-Pank, das mir mehr Material gab, als es Pander zur Verfügung gestanden hatte. Leicht ließ sich feststellen, daß die verschiedenen Arten, die Pander errichtet hatte, nicht aufrechterhalten werden können, es sind alle nur denkbaren Übergänge vorhanden. Die mikroskopische Untersuchung ergab nun, daß alle *Oniscolepis*-Reste die gleiche Struktur aufweisen wie Panders *Strosipherus*. Beide Gattungen müssen vereinigt werden. Da sich *Oniscolepis* reichlich in der bekannten Typuslokalität Ohesaare-Pank findet, besonders häufig in Panders Form *Oniscolepis dentata,* so ist der Name *Oniscolepis* vorzuziehen. Unter diesem Namen sollen auch die Reste aus dem Beyrichienkalk beschrieben werden, für die ich keinen Speziesnamen auf-

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stellen möchte. Für die Reste aus dem Ohesaare-Pank empfiehlt sich der Name *Oniscolepis dentata* Pander.

Morphologie (Abb. 10). Als Vergleichsbasis wähle ich Reste vom Typusort Ohesaare-Pank (Abb. 10 A—G), die aus einer kleinen Gesteinsprobe gewonnen wurden. Teils sind es Schuppen, teils tesseraartige Plättchen oder auch einzelne große Dentinleisten, die sich von ihrer spongiösen Unterlage abgelöst haben. Die Schuppen (Abb. 10 B und C) ähneln den Schuppen von *Corvaspis,* sind aber weniger dick, da die Unterschicht gering entwickelt ist. Die Skulpturen sind leistenförmig, vorne und hinten zugespitzt. Ihre sehr ausgeprägten Seitenzacken sind als schräge, nach vorne gerichtete Rippchen entwickelt. Meist liegen in der Mitte des skulptierten Feldes die kleinsten und schmalsten Leisten, seitlich eingefaßt von bogenförmig gekrümmten, nach außen zu immer größeren Leisten. — Die Tesserae (Abb. 10 A) sind dicke, gestreckt polygonale Plättchen mit steil abfallenden Rändern und wohlentwickelter Unterschicht. Auch sie zeichnen sich meistens dadurch aus, daß die kleinsten Dentinleisten im Zentrum der Skulpturen liegen. Viele Dentinleisten sind durch einen niedrigen medianen Kiel verziert, der aber bereits den Nachbarleisten fehlen kann. Pander errichtete für Formen mit einem medianen Kiel auf den Dentinleisten die Art *Oniscolepis dentata* zum Unterschied von Arten, denen dieses Merkmal fehlen soll. Auf ein und derselben Schuppe finden sich Dentinleisten mit und ohne Kiel, dieser Eigenschaft kommt daher keine diagnostische Bedeutung zu. — Die großen isolierten ovalen Dentinleisten mit verschieden ausgeprägten, nach vorne gerichteten Seitenzacken (Abb. 10 D—E) sind durch Übergänge aller Größen mit typischen *Oniscolepis*-Resten eng verbunden, denen sie auch histologisch bis in alle Einzelheiten gleichen. Es ist daher nicht berechtigt, sie als besondere Gattung unter dem Namen *Strosipherus* abzutrennen.

Oniscolepis-Reste finden sich in allen Schichten des Beyrichienkalkes, wenn auch stets nur zerstreut. Wesentliche Unterschiede gegenüber *Oniscolepis dentata* aus dem Ohesaare-Pank lassen sich vorläufig nicht herausstellen; ich bezeichne diese Reste als *Oniscolepis* sp. indet.

Auch die Reste aus dem Beyrichienkalk umfassen Schuppen (Abb. 10 H, M und P), Tesserae (Abb. 10 J, K und Q) und isolierte große Dentinleisten (Abb. 10 N—O). Die Anordnung und die Ausbildung der Skulpturen, die die Oberschicht bilden, ändert sich von Stück zu Stück, doch finden sich meist die kleinsten und schmalsten Dentinleisten im Zentrum (Abb. 10 J, K, L, P und Q). Die randlich umfassenden Dentinleisten können sehr lang und wesentlich breiter werden als die mittleren (Abb. 10 J—K). Manchmal sind die Leisten an der inneren, zum Zentrum gerichteten Seite weniger gezackt als an der nach außen gerichteten Seite (Abb. 10 J, M und P). Unregelmäßigkeit der Ausbildung ist geradezu ein Merkmal der *Oniscolepis*-Reste. Sehr variabel und unregelmäßig ist auch der Abstand der Leisten, dicht nebeneinander finden sich schmale und breite Zwischenrinnen (Abb. 10 J und Q, *zwr*). Die Leisten sind relativ hoch

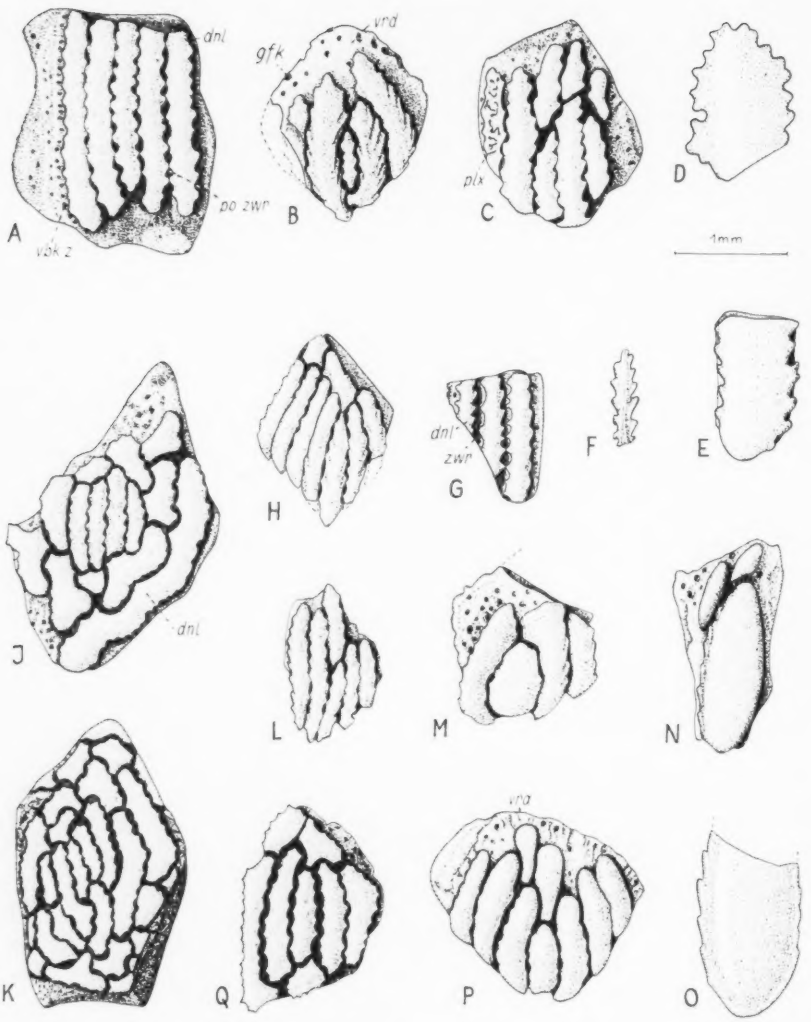

Abb. 10. *Oniscolepis* sp. indet. Tesserae, Schuppen und Dentinleisten; × 16. A Tessera; f 662. B Schuppe; f 663. C Tessera; f 664. D breite Dentinleiste; f 665. E breite Dentinleiste; f 666. F einzelne schmale Dentinleiste; f 667. G Teil einer Tessera; f 668. Fig. A—G Stücke vom Ohesaare-Pank auf Oesel, Fig. H—Q Stücke aus dem Beyrichienkalk. H Schuppe; f 669. J Tessera; f 670. K Tessera mit konzentrisch angeordneten Leisten; f 671. L Schuppenrest; f 672. M Schuppenrest mit breiter Mittelleiste; f 673. N Rest mit großen und kleinen Dentinleisten; f 674. O breite Dentinleiste; f 675. P Schuppe; f 676. Q Tessera; f 677. *dnl* Dentinleiste; *gfk* Gefäßkanal; *plx* Gefäßplexus in der Dentinleiste; *po.zwr* Poren der Zwischenrinne; *vbk.z* Verbindungskanal zur Zwischenrinne; *vrd* Vorderende; *zwr* Zwischenrinne.

und manchmal durch niedrige mediane Kiele ausgezeichnet, besonders im Zentrum der Schuppen.

Das Vorderende der Schuppen ist frei von Skulpturen und etwas verdickt. Auf den Tesserae ist dagegen die gesamte Oberfläche mit Dentinleisten bedeckt (Abb. 10 K), die eine gewisse konzentrische Anordnung haben. Die Gestalt der Tesserae ist meist gestreckt polygonal. Ihre Mittelschicht ist reticulär spongiös und relativ sehr dick. Nur an wenigen Schuppen ist die Unterschicht gut ausgebildet; die Tesserae haben meist eine recht dicke Unterschicht.

Die großen ovalen Dentinleisten findet man fast stets isoliert und von der reticulären Spongiosa abgelöst. Ihre Seitenränder zeigen verschieden deutlich ausgeprägte Randzacken, die nach vorne gerichtet sind (Abb. 10 N—O). Kielbildungen weisen die großen Leisten nicht auf, oft sind sie recht stark gewölbt. Selten sind Reste, denen große und kleine Dentinleisten aufsitzen (Abb. 10 N). Große und kleine Leisten sind durch alle Übergänge verbunden. An welchen Stellen des Panzers die großen Leisten auftreten, kann aus den kleinen Bruchstücken nicht erschlossen werden.

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Bruchstücke mit gekammerter Spongiosa oder mit Teilen der Sinneskanäle und ihren Porenmündungen habe ich bisher nicht gefunden. Die Bildung von Tesserae erinnert an den Bau des Panzers von *Corvaspis*, der die Gattung *Oniscolepis* anscheinend nahesteht.

H i s t o l o g i e (Abb. 11 und 12). Der histologische Aufbau der Reste ist sehr einheitlich, Unterschiede sind vor allem durch die oft gut erhaltenen Bildungsstadien des Dentins und Aspidins in der Oberschicht bedingt. Bei keiner anderen Heterostraci-Gattung des Beyrichienkalks finden sich die verschiedenen Bildungsstadien in so mannigfaltiger Erhaltung. Ursprünglich weite Pulpahöhlen oder Pulpakanäle verengen sich und umwanden sich mit dicken Dentin- oder Aspidinmänteln (Dentone und Aspidone).

Die U n t e r s c h i c h t (Abb. 11 B—D) ist selten deutlich von der Mittelschicht abgesetzt; sie wird von relativ wenigen aufsteigenden Gefäßkanälen durchbohrt. Sie ist ebenso wie die Mittelschicht von sehr zahlreichen Sharpeyschen Fasern erfüllt, die in der Oberschicht bis unmittelbar an das Dentin reichen können. Je nach der Dicke der M i t t e l s c h i c h t finden sich in ihr eine oder mehrere Lagen engerer oder weiterer Gefäßkanäle; Reste mit gekammerter Spongiosa habe ich bisher nicht gefunden. Die oberste Lage der Gefäßkanäle ist am Aufbau der Dentinleisten aufs engste beteiligt.

Unter den schmalen D e n t i n l e i s t e n verläuft in den frühen Stadien der Dentinbildung ein sehr weiter Längskanal (Abb. 11 A, C und G, *lgk*), der oft in auffallend regelmäßiger Weise durch Queräste die Zwischenrinnen versorgt und zugleich mit den Längskanälen der Nachbarleisten in Verbindung tritt (Abb. 11 G, *vbk.z*). Der Längskanal entsendet senkrecht oder ein wenig schräg nach oben zahlreiche Pulpakanäle (*plk*), bei ganz schmalen Dentinleisten in einer einfachen Reihe, bei breiteren Dentinleisten auch in mehreren Reihen nebeneinan-

der (Abb. 11 E—F). Die Pulpakanäle sind oben miteinander durch arkadenförmig gebogene Kanäle verbunden, die einen horizontalen Plexus (*plx*) enger Kanäle bilden (Abb. 11 E—F). Aus den Enden der Pulpakanäle und aus dem Plexus der Arkadenkanäle strahlen die Dentinröhrchen. In sehr schmalen Dentinleisten findet sich nur eine Reihe von Pulpakanälen, die in der Längsrichtung durch Arkadenkanäle verbunden sein können oder diese Verbindungen entbehren, so daß die Dentinröhrchen nur aus den Enden der Pulpakanäle büschelförmig ausstrahlen. Bei Beginn der Dentinbildung fehlten auch die Pulpakanäle und der Plexus der Arkadenkanäle, dafür reichte der breite Längskanal bis an die sich bildende Dentindecke, in die er die Dentinröhrchen entsandte. Recht gut angedeutet findet sich dieses Bildungsstadium in der Abb. 11 A. Hier sind die Dentinleisten der Form nach bereits voll enwickelt, aber der Dentinmantel ist nur dünn, da die Pulpakanäle sich erst gerade zu differenzieren beginnen.

Die Gefäßkanäle der Mittelschicht treten mit den Längskanälen unter den Dentinleisten nur spärlich durch senkrecht einmündende Kanäle (*gfk.mü*) in Verbindung (Abb. 11 G). Die Verbindungskanäle (*vbk.z*) zu den Zwischenrinnen (Abb. 11 A, B, D und G) erheben sich ein wenig nach oben und münden (*vbk.mü*) schräg seitlich in den Boden der Zwischenrinnen. In den meisten Fällen verbinden sie sich gleichzeitig mit dem entsprechenden Kanal der Nachbarleiste (Abb. 11 D). Die Zwischenrinnen haben einen sehr charakteristischen birnförmigen Querschnitt, der durch einen augeprägten Absatz — ähnlich wie bei *Corvaspis* — unterteilt wird (Abb. 11 A, B und D). Unmittelbar über dem Absatz ist die Zwischenrinne am breitesten, darunter wird sie wesentlich schmaler. Je nach dem Abstand der Dentinleisten ist der Mündungsspalt der Zwischenrinne verschieden breit.

Die Dentinröhrchen sind meist sehr regelmäßig parallel zueinander angeordnet, nur die am weitesten seitlich stehenden Röhrchen sind unregelmäßig gestaltet (Abb. 12 H). Alle Dentinröhrchen vergabeln sich auf gleicher Höhe (Abb. 12 D—G) und lösen sich etwas höher in mehrere Ästchen auf. Durch die Regelmäßigkeit der Vergabelung und Verästelung ist das Dentin oft sehr deutlich geschichtet. Die oberste Lage mit den relativ langen Endästchen ist hell und klar; auf der Höhe der Vergabelung sammeln sich oft bituminöse Verunreinigungen, so daß diese Zone durch schwarze Flecken gekennzeichnet ist (in den Abbildungen nicht eingezeichnet). Die Lamellierung des Dentins ist oberhalb der Vergabelung undeutlich oder gar nicht sichtbar, sehr gut ausgeprägt dagegen unterhalb der Vergabelung, wo sie kontinuierlich in die Lamellierung des Aspidins übergeht (Abb. 12 A).

Durch die zunehmende Aspidinbildung wird auch der breite Längskanal unter den Dentinleisten aufgelöst und verengt. Das Aspidin trägt ursprünglich die Dentinleiste, deren Seitenwand sie bildet. Durch die queren Verbindungskanäle wird die Seitenwand in „Säulen" zerlegt. Allmählich verbinden sich viele dieser "Säulen" und überspannen oder trennen den Längskanal, der zum Schluß in Teil-

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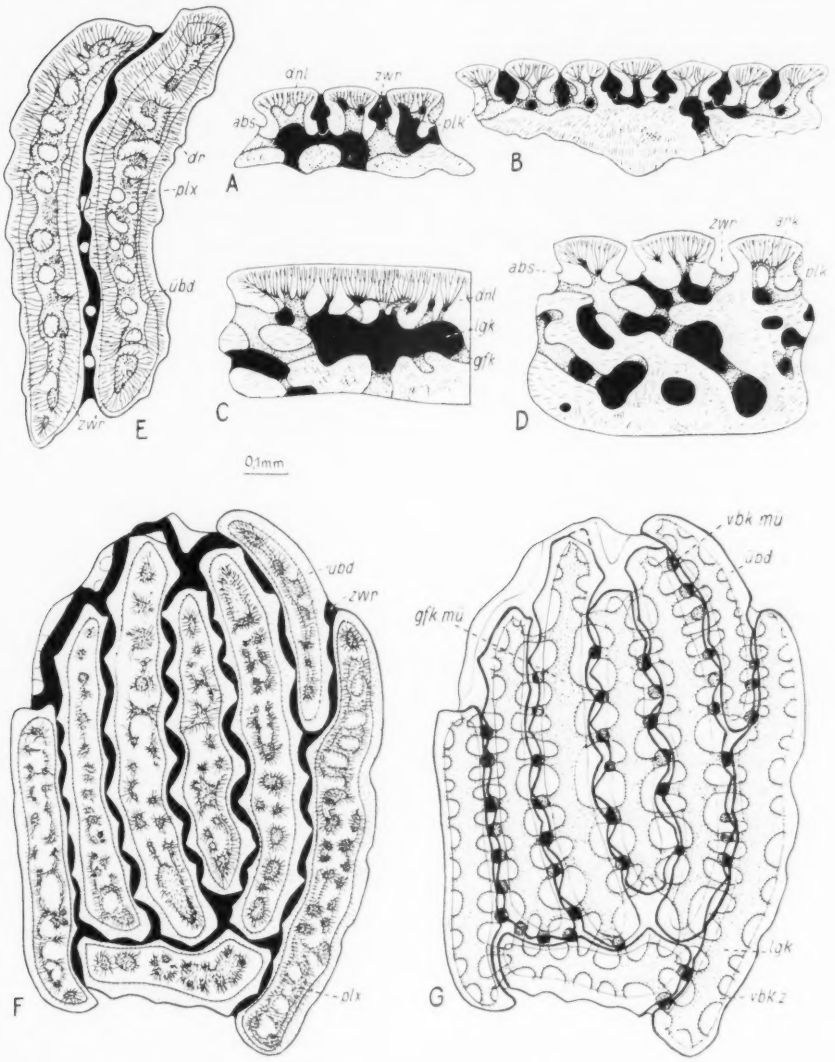
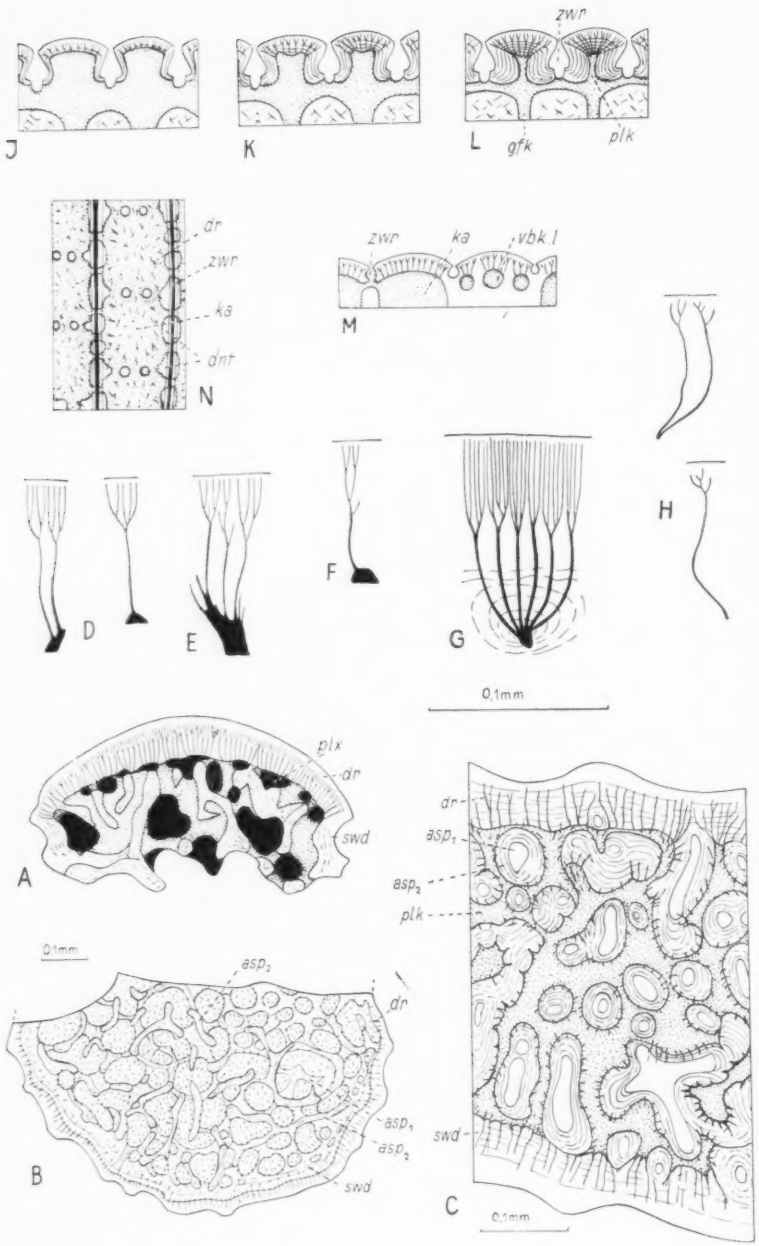


Abb. 11. *Oniscolepis* sp. indet. Dünnschliffe; × 65. A Schliff Nr. 2616 Berlin; vertikaler Querschnitt durch Schuppe. B Schliff Nr. 2615 Berlin; vertikaler Querschliff durch Schuppe. C Schliff Nr. 2190 Berlin; vertikaler Längsschliff durch Schuppe. D Schliff Nr. 2618 Berlin; vertikaler Querschliff durch Tessera. E Schliff Nr. 2611 Berlin; Horizontalschliff durch zwei Dentinleisten. F und G Schliff Nr. 2609 Berlin; Horizontalschliff durch die Dentinleisten bei hoher (F) und bei tiefer Einstellung (G). *abs* Absatz in der Zwischenrinne; *ark* Arkadenkanal; *dnl* Dentinleiste; *dr* Dentinröhrchen; *gfk* Gefäßkanal; *gfk.mü* Mündung von aufsteigenden Gefäßkanälen in die Zwischenrinne; *lgk* Längskanal unter den Dentinleisten; *plk* Pulpakanal; *plx* Plexus der Arkadenkanäle; *übd* Überdachung der Zwischenrinne; *vbk.mü* Mündung der Verbindungskanäle in die Zwischenrinne; *vbk.z* Verbindungskanal zur Zwischenrinne; *zwr* Zwischenrinne.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abschnitte zerlegt und sehr eingeengt wird (Abb. 11 B und D). Grundsätzlich die gleichen Erscheinungen müssen sich bei der Bildung von Dentinskulpturen immer einstellen, aber nur selten sind alle Stadien fossil erhalten.

Die Abbildungen 12 J—K geben rein schematisch wieder, wie sich die Dentinleisten bilden. Zu Beginn sind es sehr dünnwandige Gebilde mit sehr weitem Hohlraum des quergetroffenen Längskanals (Abb. 12 J), das Dentin bildet nur eine dünne Decke, die die Enden der Dentinröhrchen einschließt. Allmählich verdicken sich die Dentindecke und die Aspidin- oder Dentinseitenwände (letztere meist ohne, selten mit vereinzelten Dentinröhrchen); dieses Stadium (Abb. 12 K) findet sich schon in fossiler Erhaltung (Abb. 11 A). Die Abb. 12 L gibt das Endstadium wieder, bei der alle Kanäle wohldifferenziert und eng geworden sind. Die ursprünglich weiten Hohlräume unter und in den Dentinleisten enthielten vermutlich bereits die Gefäßkanäle des Endzustandes, aber rings umgeben von unverkalktem, noch kolloidalem Dentin.

Die großen ovalen Dentinleisten, die früher als *Strosipherus* bezeichnet worden sind, haben den gleichen histologischen Aufbau und zeigen ebenfalls alle Bildungsstadien. Auch die Dentinröhrchen sind ebenso regelmäßig gestaltet. Unter den großen Dentinleisten verläuft naturgemäß kein einzelner Längskanal, sondern ein Kanalnetz im schwammartigen Aspidin (Abb. 12 A). Zuerst werden die Dentindecke und die Seitenwände der Leiste gebildet, die innen einen großen Pulpahohlraum enthält. Alsbald verdickt sich die Dentindecke und an ihrer Unterseite entstehen feine Aspidinbälkchen unregelmäßiger Gestalt (Abb. 12 B), die keine deutliche Lamellierung (asp_1) aufweisen. Zwischen ihnen dehnen sich weite Hohlräume von unregelmäßiger Gestalt. Auf diese Bälkchen legt sich anschließend in immer zunehmender Dicke feinlamelliertes Aspidin (asp_2) und verengt dadurch schrittweise die Hohlräume (Abb. 12 C), bis sie zu engen Kanä-

Abb. 12 A—L. *Oniscolepis* sp. indet. Dünnschliffe. A Schliff Nr. 2199 Berlin; vertikaler Querschnitt durch breite Dentinleiste; × 65. B Schliff Nr. 2191; Horizontalschliff durch junge breite Dentinleiste mit dünner Dentindecke und einsetzender Spongiosabildung; × 65. C Schliff Nr. 496 Berlin; Horizontalschliff durch breite Dentinleiste mit primärem und sekundärem Aspidin; × 125. D—G aufsteigende, H horizontale Dentinröhrchen; × 225; D Schliff Nr. 2608 Berlin; E und F Schliff Nr. 2196 Berlin; G Schliff Nr. 489 Berlin; H Schliff Nr. 2611 Berlin. J—L Schema der Einengung pulpahöhlenartiger Hohlräume in jungen Dentinleisten zu Pulpakanälen in älteren Dentinleisten; etwa × 65. M und N *Tolypelepis undulata* Pander. Schematische Abbildungen vom Aufbau der Dentinleisten; nach den Originalen Stensiös (1957); etwa × 65. M Querschnitt durch junge Dentinleisten, rechts Zwischenwand der Spongiosa mit drei verbindenden Längskanälen getroffen. N Aufsicht auf die Dentinleisten mit ihren Spongiosakammern, aus denen die Dentinröhrchen ausstrahlen, mit Längsverbindungskanälen und Querkanälen zur Nachbarleiste und Zwischenrinne; das Dentin zwischen den Längsverbindungen der Kammern erscheint im Auflicht dunkel, täuscht aufsteigende Kanäle zur Spongiosakammer vor. asp_{1-2} primäres und sekundäres Aspidin; *dnt* Dentin; *dr* Dentinröhrchen; *gfk* Gefäßkanal; *ka* Spongiosakammer bzw. Pulpahöhle; *plk* Pulpakanal; *plx* Gefäßplexus über den Pulpakanälen; *swd* Seitenwand der Dentinleiste; *vbk.l* Längsverbindungskanal der Spongiosakammern, der Dentinröhrchen ausstrahlt; *zwr* Zwischenrinne.

len werden. An der Seitenwand (*swd*) der Leiste geht das Dentin mit seinen Lamellen kontinuierlich in das Aspidin über, das sich vom Dentin nur durch das Fehlen der Dentinröhrchen unterscheidet. Die ersten Bildungsstadien sind wegen ihrer Zartheit seltener erhalten als die späteren. Der in der Abb. 12 B wiedergegebene Rest hat eine größtenteils noch so dünne Dentindecke, das sie nur das Dentin oberhalb der Vergabelung der Dentinröhrchen umfaßt. Trotzdem bilden sich bereits die ersten Aspidinbälkchen unterhalb des Dentins, an das sie gelegentlich schon heranreichen.

M a ß e. Die Breite der Dentinleisten schwankt zwischen 100 bis 1650 μ. Die Tesserae können 875 μ dick werden. Die quergerichteten Verbindungskanäle zu den Zwischenrinnen sind etwa 30 μ breit. Der Durchmesser der Pulpakanäle beträgt 8—25 μ. Die Mündungsbreite der Zwischenrinnen kann 15—30 μ betragen, die Tiefe der Zwischenrinnen 80 bis 110 μ, die maximale Breite unmittelbar über dem Absatz etwa 45 bis 85 μ.

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TOLYPELEPIS UNDULATA PANDER

Hin und wieder finden sich in verschiedenen Stücken des Beyrichienkalks kleine Reste eines Heterostracen, die an *Oniscolepis* erinnern, aber etwas breitere und niedrigere Dentinleisten haben, die nur durch sehr schmale, fast verdeckte Zwischenrinnen getrennt werden. Sie erinnern an den von PANDER (Taf. 6 Fig. 32) als *Oniscolepis magna* beschriebenen, höchstwahrscheinlich mit *Tolypelepis* identischem Rest vom Ohesaare-Pank auf Oesel. Mir liegt für eine Klärung dieser Frage zu wenig Material aus den Beyrichienkalken und vom Ohesaare-Pank vor.

Gelegentlich eines Besuches in Stockholm konnte ich die von STENSIÖ (1957) abgebildeten Panzer von *Tolypelepis* unter dem binokularen Mikroskop untersuchen und dabei die Angaben BYSTROWS (1955, S. 481—485, Abb. 10 und 11) prüfen; Dünnschliffe stehen mir leider nicht zur Verfügung. Die Dentinleisten weisen noch sehr weite, jedoch gekammerte Hohlräume auf mit recht dünner Dentindecke. Die Hohlräume sind mit hellem Kalk erfüllt, so daß ihr Umriß sehr deutlich unter dem Dentin zu erkennen ist. Die Hohlräume ähneln weitgehend den Hohlräumen der in der Abb. 7 L und M wiedergegebenen Reste von *Anglaspis* sp., nur sind sie relativ länger und schmaler. Die Hohlräume einer Leiste verbinden sich an ihren kurzen Enden miteinander durch zwei bis drei hochgelegene Kanälchen (Abb. 12, M und N), aus denen ebenfalls Dentinröhrchen strahlen. Diese Verbindungskanäle durchbrechen die Kammerwände, die die Hohlräume trennen (Abb. 12 M). Das durchsichtige Aspidin zwischen den Verbindungskanälen läßt das auffallende Licht hindurch, es erscheint daher dunkel im Gegensatz zu dem hell reflektierenden Kalk der Hohlraumausfüllung. In der Aufsicht unter den Leisten erscheinende Querreihen dunkler Punkte stellen die sichtbaren Teile der Querwände dar, nicht aber aufsteigende Kanäle, als

welche sie versehentlich bei Stensiö (1957, Abb. 170 A, *f.bc*) bezeichnet worden sind.

Bystrows Beschreibung gibt Dentinleisten in sehr frühen Bildungsstadien wieder, die angeblich von einem einzigen durchgehenden Hohlraum ohne Querwände unterlagert werden (Bystrow 1955, Abb. 12). Die von Stensiö (1957) abgebildeten Stücke zeigen bereits deutlich die Bildung von Querwänden, so daß der Hohlraum unter den Dentinleisten in getrennte Kammern zerfällt. Jede dieser Kammern wird in ihrer Mitte den Pulpakanal bzw. den Gefäßkanal enthalten haben, aus dessen Oberende die Dentinröhrchen strahlen. Daß die Dentinröhrchen auf ein Zentrum konvergieren, kann man an den Originalen Stensiös leicht wahrnehmen. *Tolypelepis* weicht im Bau der Dentinleisten nicht von den übrigen Gattungen der Cyathaspida ab. Die etwas schematisierten Abbildungen Bystrows geben nur eine bestimmte Stelle eines einzelnen Restes wieder, auch *Tolypelepis* wird nicht an allen Stellen des Panzers völlig gleich gebaut sein und wird die verschiedenen Stadien der Dentinbildung aufweisen.

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Osteostraci

Die Osteostraci sind im Beyrichienkalk und den ihm auflagernden Gesteinen wesentlich seltener als die Heterostraci. Kleine Plättchen, die mit sternförmigen Tuberkeln besetzt sind, gehören höchstwahrscheinlich zur Acanthodier-Gattung *Nostolepis*. Sie müssen noch näher untersucht werden. Dagegen sind die von Brotzen als „*Porolepis*" und von mir (Gross 1956) als Knochenplättchen incertae sedis beschriebenen Bruchstücke Teile von Schuppen oder vom Panzer einer Osteostracen-Gattung, die ich nachfolgend als *Zenaspis* ? sp. indet. bezeichne, da die Skulptur sehr an die der Lankesterschen Gattung erinnert. *Zenaspis* ? sp. indet. findet sich bereits vereinzelt in den dolomitischen oberen Beyrichienkalken, häufig ist sie aber nur in den Geschieben Bey. 36 und 37 zusammen mit den Resten von *Traquairaspis, Anglaspis* und *Corvaspis*. Besonders schöne Bruchstücke und Schuppen fanden sich in einem weiteren Geschiebe (Bey. 38), dem die genannten Heterostraci fehlen, das aber erstmalig schön erhaltene Schuppen von Anaspiden lieferte (Gross 1958). Eine vermutlich selbständige, vorläufig noch unbekannte Osteostraci-Gattung findet sich recht zahlreich in den Geschieben Bey. 36 und 37, leider nur in kleinen Bruchstücken. In anderen Geschieben habe ich diese Form bisher nicht gefunden, sie wird nachfolgend als Osteostraci: genus indeterminabile beschrieben.

ZENASPIS LANK. ? SP. INDET.

Brotzen (1934) entdeckte in dem Geschiebe Bey. 36 Panzerreste mit zahlreichen Poren in der Oberschicht, die er zu *Porolepis* stellte. Die Anwesenheit von *Porolepis* sollte das unterdevonische Alter des Geschiebes beweisen. Viele weitere

Reste gleichen Aufbaus fand ich bei der Auflösung des Geschiebes Bey. 36 in Essigsäure. Ich beschrieb den histologischen Aufbau dieser Reste kürzlich (Gross 1956) als „Knochenplättchen incertae sedis (*Poracanthodes* ?)", ohne eine Entscheidung über die systematische Zugehörigkeit zu den Osteostraci oder den Acanthodii herbeiführen zu können. Das komplizierte Porenkanalsystem erinnerte sehr an das der Osteostraci, die mehrfache Dentinbildung an die Acanthodii. Eine geschlossene Dentindecke über einer älteren Lage von Dentinskulpturen war von den Osteostraci unbekannt. Mir schien die Deutung der Reste als Plättchen vom Exocranium eines Acanthodiers (*Poracanthodes*) etwas eher berechtigt als die Zuweisung zu den Osteostraci.

Sehr viele Reste gewann ich Anfang 1957 durch die Auflösung der Geschiebe Bey. 37 und Bey. 38. Während sich die Reste aus dem Geschiebe Bey. 37 das dem Geschiebe Bey. 36 völlig gleicht, vorzüglich für die histologische Untersuchung eignen, sind die Reste aus dem Geschiebe Bey. 38 für die histologische Untersuchung kaum brauchbar, dafür zeigen sie viel mehr von der Skulptur und der Gestalt. Unter letzteren Resten fanden sich fast intakte Rumpf-Schuppen, die mit einem Schlage die Zugehörigkeit der Reste zu den Osteostraci bewiesen. Bei einem Besuch in Stockholm (Sommer 1957) legte ich meine Schliffe Dr. Ørvig vor, der sie sogleich als zu den Osteostraci gehörig erkannte. Das schöne Vergleichsmaterial der Schliffsammlung Dr. Ørvigs gab mir endlich die Gelegenheit, den histologischen Aufbau vieler Cephalaspiden-Gattungen kennenzulernen; mein eigenes Material umfaßte fast ausschließlich Reste der Gattung *Trematapis*. Ferner wies mich Dr. Ørvig auf die Ähnlichkeit der Skulpturen der Reste aus den Geschieben mit denen der Art *Cephalaspis excellens* Wängsjö (Wängsjö 1952 Taf. 40 Fig. 4) hin, die nach Stensiös System zur Gattung *Zenaspis* Lank. gehört (Stensiö 1957). Es kann natürlich allein auf Grund der Skulpturen nicht mit Sicherheit die Einordnung der Reste aus den Geschieben in die Gattung *Zenaspis* vorgenommen werden, die Bezeichnung *Zenaspis* ? sp. indet. soll nur auf die einzige feststellbare Ähnlichkeit hinweisen. Noch weniger kann an eine Bestimmung der Art gedacht werden. Die Beschreibung der Reste wird durch die ausgezeichnete Erhaltung der Bildungsweise des Dentins gerechtfertigt.

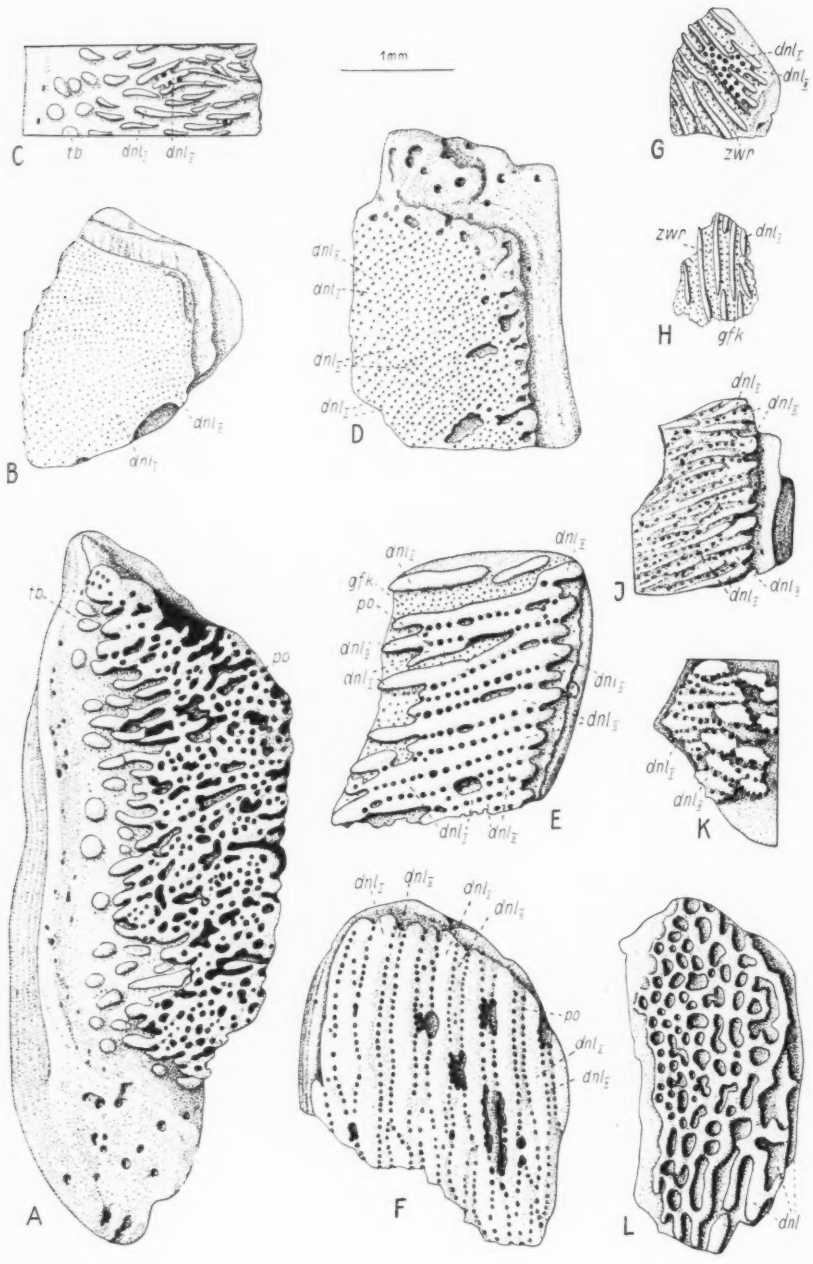
Morphologie und Skulpturen (Abb. 13). Fast alle Reste sind Bruchstücke von Schuppen und vom Kopfschild. Nur ganz wenige Schuppen sind unversehrt, Tesserae sind überhaupt nicht gefunden worden. Die Schuppen der Rumpfflanken sind kurz und hoch, am Vorderrand ohne ausgeprägte Überlagerungsfläche recht steil abfallend (Abb. 13 A), am Oberende und am Unterende zugespitzt und abgeflacht. Der hohlen Unterseite fehlt jede versteifende Mittelrippe, so daß sich die Schuppen bei aller äußerlich weitgehender Ähnlichkeit leicht von denen der Anaspida (Gross 1958 Taf. 1 und 2) unterscheiden lassen. Die Schuppen von *Zenaspis* ? sp. indet. sind viel kräftiger als die Schuppen der Anaspida; ihre Unterseite ist flach ausgehöhlt.

Von besonderem Interesse ist der Bau der Oberschicht bzw. der Skulpturen, der ungewöhnlich verschiedenartig sein kann. Manche Reste haben eine geschlossene Oberschicht aus Mesodentin, die von zahlreichen Porenkanälen durchbohrt wird. Solche Reste erinnern an die Panzer von Trematapiden. Aber bei näherer Betrachtung erkennt man meist, daß unter der geschlossenen Dentindecke langgestreckte Skulpturen als Streifen hindurchschimmern (Abb. 13 B und D); es fehlen die für die *Trematapis* so charateristischen polygonalen Maschen des Porenkanalsystems. Dafür sind bei *Zenaspis* ? sp. indet. die Porenkanäle und die dazugehörigen Maschenkanäle in schrägen Längsreihen parallel zu den durchschimmernden Skulpturen angeordnet (Abb. 13 B, D, E und F).

Andere Reste, die sich häufiger finden, haben eine freie Oberfläche der Mittelschicht, die mit zahlreichen schräg von vorne oben nach hinten unten verlaufenden schmalen Dentinleisten besetzt ist, zwischen denen viele Blutgefäßkanäle (*gfk*) münden (Abb. 13 C, G und H). Diese Dentinleisten (dnl_I) sind wallartig gestaltet, mit schräg oder steil abfallenden, selten etwas hohlen Seitenflächen ohne Seitenzacken. Der Kamm der Leiste läßt bei starker Vergrößerung eine feine Schrägstreifung erkennen, die nach vorne gerichtet ist (Winkel nach vorne offen) wie alle derartigen Streifen und Leistchen bei Agnathen und Fischen (z. B. *Glyptolepis, Moythomasia* u.a.). Die Dentinleisten sind vorne verdickt (Abb. 13 A, C und J) und niedrig, hinten werden sie kommaförmig schmal und spitz, ihre Hinterenden sind am höchsten und können über den Hinterrand der Schuppen herausragen. Längs des Vorderrandes sind die Skulpturen meist rundliche flache Tuberkel (Abb. 13 A und C, *tb*), ganz ähnlich wie auf den Schuppen der Anaspida. Die eben geschilderten Dentinleisten bilden die erste Skulpturgeneration oder die primäre Oberschicht.

Meist findet sich aber eine zweite Mesodentingeneration in allerverschiedenster Ausbildung. Das Mesodentin der zweiten Generation (dnl_{II}) ist oft schon durch die geringere Durchsichtigkeit und kräftigere Färbung von der ersten Generation zu unterscheiden; im Auflicht ist das sekundäre Dentin heller, weil es mehr Licht zurückwirft. Oft sind die Grenzen beider Dentingenerationen sehr scharf zu erkennen. Besonders hervorgehoben sei der Umstand, daß nur im sekundären Dentin das Porenkanalsystem in Erscheinung tritt. Es war sicher bereits zwischen den Dentinleisten der ersten Generation (dnl_I) vorhanden, aber es wurde nicht von Hartgewebe umschlossen, so daß sich keine Spuren von ihm erhalten konnten.

Die Abb. 13 C gibt einen kleinen Ausschnitt aus einer großen, vollständigen Schuppe, die fast nur mit Dentinleisten der ersten Generation besetzt ist. An einigen wenigen Stellen erkennt man erste Spuren des sekundären Dentins in Gestalt von Querspossen zwischen den primären Dentinleisten (Abb. 13 C, rechts unten) oder in Gestalt einer sekundären Dentinleiste, die sich durch Querspossen mit den benachbarten primären Dentinleisten verbindet (Abb. 13 C, Mitte oben).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Zwischen den Querspossen öffnen sich die Porenkanäle, die damit sichtbar in Erscheinung treten. Bereits weiter fortgeschritten sehen wir diese Bildungen in der Abb. 13 G, wo sich die vertieften Furchen zwischen den primären Dentinleisten mit sekundärem Dentin füllen, das selber neue Dentinleisten (dnl_{II}) bildet. Eine Weiterentwicklung ist die Bildung einer sekundären Dentingeneration auf der in der Abb. 13 A wiedergegebenen Schuppe. Hier sind schon die meisten Furchen zwischen den primären Dentinleisten mit sekundärem Dentin ausgefüllt, das mehr Fläche einnimmt als das primäre Dentin. Wiederum eine Fortbildung ist das sekundäre Dentin anderer Schuppenreste (Abb. 13 E und J). In der Abb. 13 E ist das primäre Dentin leicht vom sekundären Dentin zu unterscheiden, die Anordnung der primären und sekundären Leisten ist sehr regelmäßig. Die primären Leisten des abgebildeten Restes sind schmaler und niedriger als die sekundären Leisten, zu denen auch die Querspossen gehören, denn die ursprünglichen Furchen zwischen den primären Leisten sind breiter als diese. In den breiten Zwischenfurchen (*zwr*), die nun von den sekundären Leisten überdeckt werden, müssen zwei Maschenkanäle gelegen haben, da die sekundären Leisten von zwei Porenkanal-Reihen begleitet werden. Die Abb. 13 F gibt einen Schuppenrest wieder, der von einer geschlossenen Oberschicht bekleidet wird. Aber die Oberschicht läßt sehr deutlich ihre Zusammensetzung aus primären und sekundären Dentinleisten erkennen. Die primären Dentinleisten sind stets dunkler und in den meisten Fällen schmaler als die sekundären Dentinleisten. Die Vorderenden der sekundären Leisten gleichen, abgesehen von ihrer größeren Breite, ganz denen der primären Leisten. Aber nie zeigen die sekundären Leisten die feine nach vorne gerichtete Riefung der primären Leisten.

Mit seinen Querspossen grenzt das sekundäre Dentin an die primären Leisten, ohne jemals mit ihnen zu verschmelzen. Bei Querspossen mit weitem Abstand berühren ihre an die primären Leisten angrenzenden Enden einander nicht (Abb. 17 B). Bilden sich höhere sekundäre Leisten mit geringem Abstand der Querspossen, so fließt das sekundäre Dentin der Sprossenenden an den Seitenwänden

Abb. 13. *Zenaspis* ? sp. indet. Schuppen- und Panzerreste; × 16. A Schuppe mit in Bildung begriffener zweiter Dentingeneration (aus zeichnerischen Gründen Oberende nach unten gerichtet); f 678. B Schuppenrest mit dickerer sekundärer Dentindecke, durch die noch einige primäre Dentinleisten hervorschimmern; f 679. C Ausschnitt aus einer großen Schuppe mit primären Dentinleisten und ersten Dentinbildungen einer zweiten Generation; f 680. D Schuppenbruchstück mit primären und sekundären Dentinleisten gleicher Höhe; f 681. E Schuppenbruchstück mit weit fortgeschrittener Bildung breiter sekundärer Dentinleisten zwischen den schmalen primären; f 682. F Schuppenbruchstück mit breiten primären und schmalen sekundären Dentinleisten; f 683. G Schuppenbruchstück mit verstreuter sekundärer Dentinbildung; f 684. H Schuppenbruchstück mit ausschließlich primären Dentinleisten; f 685. J Schuppenbruchstück mit sekundärem Dentin in Gestalt von Querspossen zwischen den primären Dentinleisten; f 686. K Panzerbruchstück mit unregelmäßig übereinander gelagerten Dentinleisten erster und zweiter Generation; f 687. L Panzerbruchstück mit Netz aus primären und sekundären Dentinleisten; f 688. dnl_{I-II} primäre und sekundäre Dentinleisten; *gfk* Gefäßkanal; *po* Mündung der Porenkanäle; *tb* Dentintuberkel; *zwr* Zwischenfurche.

der primären Leisten zusammen. Doch dabei bleiben die Möglichkeiten nicht stehen. Das sekundäre Dentin der Querspossen beginnt auf die primären Leisten überzugreifen und kann sie völlig überdecken (Abb. 13 B, Abb. 17 D). Es entsteht eine geschlossene sekundäre Dentindecke von verschiedener Mächtigkeit. Nur bei der Benutzung heller Lichtquellen kann man dann noch die primären Leisten unter der Decke durchschimmern sehen. Zum Schluß sind die primären Dentinleisten im Auflicht nicht mehr zu entdecken, erst im Dünnschliff wird ihr Vorhandensein sichtbar (Abb. 17 E). Solche Stücke mit völlig geschlossener sekundärer Dentindecke sind dann äußerlich nicht von Resten zu unterscheiden, die nur eine primäre geschlossene Dentindecke haben, unter welcher keine Dentinleisten sich befinden.

Nicht immer sind die sekundären Dentinleisten von den primären an der Farbe, Helligkeit oder der Gestalt sicher zu unterscheiden. Doch findet man andere Unterschiede, wenn man genauer hinsieht. Alle Dentingebilde wachsen von oben nach unten, von außen nach innen. Die oberste und äußerste Lage ist stets die erste Bildung, sie kann nicht mehr durch äußere Aufschichtung verdickt werden. Die Unterschiede der Bildungen des Dentins werden durch den Grad der Dentinverdickung an der Unterseite der ersten Dentinanlage bedingt. Wir dürfen also nicht annehmen, daß etwa eine sekundäre Dentindecke, die wir finden, allmählich hätte nach oben verdickt werden können. Ebensowenig konnten vorhandene primäre oder sekundäre Dentinleisten sich seitlich oder oben verbreitern oder verdicken. Wohl aber waren alle Dentinbildungen, die über Hohlräumen lagen, fähig, sich nach unten auf Kosten des Hohlraumes zu verdicken. In dieser Hinsicht finden wir verschiedene Stadien der Dentinbildung der Skulpturen.

Ganz einfache Bildungen sekundären Dentins sind die Sprossen, die zwei benachbarte primäre Dentinleisten verbinden und zwischen sich Öffnungen für die Porenkanäle aussparen. Diese Querspossen überbrücken die Furche zwischen den primären Leisten, erreichen aber nicht den Boden der Furche (Abb. 17 B). Ist der Abstand der primären Leisten zu weit, so entsteht zwischen ihnen eine sekundäre Leiste, die zu Beginn der Bildung die Zwischenfurche nur überdacht, bei weiterer Verdickung aber den Boden der Zwischenfurche erreicht und sich auf ihn stützt (Abb. 17 C, links). Man kann leicht die verschiedenen Bildungsstadien an größeren Resten finden. Im Querschnitt — etwa auf Bruchflächen — sieht demnach eine sekundäre Leiste ganz anders aus als eine primäre (Abb. 17 A—C). Die primäre Leiste hat etwa den Querschnitt eines steileren oder flacheren Walles (Abb. 17 A), die sekundäre Leiste dagegen sieht im Querschnitt etwa pilzförmig (Abb. 17 C) aus. Die stützenartige Auflage der sekundären Leiste ($dnl_{II}st$) auf den Boden der Zwischenrinne liefert den „Stiel", die Seitenteile und die Querspossen den „Hut" des Pilzes. Erreicht eine sekundäre Dentinleiste nicht die benachbarte primäre Dentinleiste, indem sie keine Querspossen bildet, so überwölbt sie einen Teil der Zwischenfurche dachartig (z. B. Abb. 13 E, Abb.

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17 C), was man nie bei einer primären Dentinleiste finden wird. Die zarten Anfangsstadien der Dentinbildung sind fossil kaum erhalten.

Seltener sind Reste mit einer groben netzartigen Skulptur (Abb. 13 L), die aber bei näherer Untersuchung ebenfalls eine Zusammensetzung aus primären Dentinleisten und kürzeren sekundären Dentingebilden zeigt, die vielfach Querverbindungen herstellen. Nur tritt bei dieser Art der Skulptur nicht das Porenkanalsystem hervor, dessen Porenkanäle im Weichgewebe zwischen den Skulpturleisten lagen. An Bruchstücken des Cornu (nicht abgebildet) sind die Flächen mit einer von zahlreichen Porenkanälen durchbohrten Dentindecke bekleidet, die Kanten hingegen mit hohen und breiten Dentinleisten, zwischen denen sich breitere Porenkanäle öffnen. Auf kürzeste Entfernung ändert sich die Skulptur: Dentindecken gehen in Leisten- oder in Netzskulptur über. Einen Rest mit tertiären, unregelmäßig über primären und sekundären Dentinleisten liegenden Dentintuberkeln gibt die Abb. 13 K wieder. Die dritte Generation unterscheidet sich aber nicht histologisch von der zweiten Generation, sondern nur in der Zeitlichkeit der Bildung. Die Skulpturen der zweiten Generation brauchten nicht alle zu gleicher Zeit zu entstehen. Dadurch, daß sich das sekundäre Dentin manchmal unter den schräg aufragenden Hinterenden der primären Dentinleisten bildete, konnten die Spitzen der primären Dentinleisten frei herausragen oder über dem sekundären Dentin liegen. Damit ist aber die Mannigfaltigkeit nicht erschöpft. Skulpturen, wie sie Wängsjö (1952 Taf. 40 Fig. 4) abbildet, finden sich ebenfalls. Die Verschiedenheit der Ausbildung der Skulptur täuscht die Anwesenheit von Resten mehrerer Gattungen in den Geschieben vor.

Die Bildung des Dentins erfolgt von den Blutgefäßen aus, die senkrecht oder schräg nach oben gerichtet sind und damit zu Pulpakanälen werden. Die Mündungen der zahlreichen Gefäßkanäle (*gfk*) in den Zwischenfurchen (Abb. 13 E, G und H) dienten nicht nur der Versorgung des Porenkanalsystems sondern ebenso der des entstehenden sekundären Dentins. Die randlichen und die zentralen Gefäßkanäle der Zwischenrinnen waren insbesondre der Dentinbildung und Dentinversorgung vorbehalten, wie im histologischen Teil weiter unten gezeigt wird.

Dentinbildungen einer zweiten Generation bei Cephalaspiden hat als erster Ørvig (1951, Fig. 11 B) beschrieben; einen weiteren Befund gab Wo. Schmidt (1954 Taf. 6 Fig. 2 d) bekannt. Es schlossen sich meine Beschreibung der Knochenplättchen incertae sedis an (Gross 1956 S. 112—117; Abb. 99—104; Taf. 14 Fig. 5), die sich nun als Knochenreste von *Zenaspis* ? sp. indet. erweisen. Das Unerwartete ist nun bei *Zenaspis* ? die große Ausdehnung und die Mannigfaltigkeit der Gebilde einer zweiten und gelegentlich auch dritten Dentingeneration. Im Enderfolg erinnert die Bildung einer sekundären Dentindecke über der urpsrünglichen, mit primären Dentinleisten besetzten Oberfläche an die Verhältnisse bei *Porolepis*. Das ursprünglich in der Cutis über der primären Ober-

fläche des Knochens liegende Porenkanalsystem wird in Hartgewebe aus Dentin eingeschlossen.

Wenn im Verlauf der Phylogenie der Cephalaspida anstelle der geschlossenen Dentindecke zerstreute Dentintuberkel treten — und dieser Vorgang hat höchstwahrscheinlich tatsächlich stattgefunden — so stellen sie manchmal Reststücke der geschlossenen Dentindecke dar, meist aber Skulpturen, die ontogenetisch vor der Dentindecke gebildet wurden, gewissermaßen als phylogenetische Neuerwerbung. Ihre Entstehung gab vielleicht den Anreiz zur Rückbildung und den späteren völligen Verlust der Dentindecke. Die primären Dentinleisten sind vermutlich primär nur im ontogenetischen Sinn, nicht im phylogenetischen, denn phylogenetisch tauchen sie später auf als die geschlossenen Dentindecken. Ebenso mag der Vorgang bei den Porolepiden gewesen sein: erst Schuppen nach Art der Osteolepiden mit geschlossener Dentindecke, danach ontogenetisches Auftreten von isolierten Hautzähnen (= Dentintuberkel) vor der Bildung der Dentindecke (Vorverlegung der Bildung), danach Verlust der Dentindecke über den Dentintuberkeln wie bei *Laccognathus*. Den endgültigen Abschluß bildet das Verschwinden aller Dentinskulpturen von der Oberfläche der Knochen und Schuppen (*Holoptychius*). Die Dentintuberkel oder Leisten sind nicht Überreste der Dentindecke, sondern sie sind der Anlaß zur Reduktion oder zum Verlust der Dentindecke. Die Dentintuberkel von *Porolepis* sind keine Erinnerung an einen ehemaligen *Laccognathus*- oder *Glyptolepis*-artigen Zustand, sondern sind dessen Ankündigung und Vorbereitung. Man kann diesen Vorgang als proterogenetisch bezeichnen, da die Bildung der Dentinskulpturen im Verlauf der Ontogenese nicht an die Bildung der phylogenetisch älteren Dentindecke anschließt, sondern ihr vorausgeht. — Dieser Gedanke ist vorläufig noch Hypothese, wir kennen nur von wenigen Cephalaspiden die Histologie des Exoskelettes, und wir kennen nicht ältere Cephalaspiden als die Gattungen aus dem Ludlow. Die Reihen sind zu unsicher und zu kurz. Mag in der zu *Zenaspis* ? sp. indet. führenden Reihe die phylogenetische Entwicklung von einer geschlossenen Dentindecke über ein Stadium mit heterochron primären Dentinleisten unter der geschlossenen Dentindecke zu einem Endzustand ohne Dentindecke aber mit Dentinleisten führen, so könnten in anderen Reihen vielleicht die Dentinleisten nicht nur phylogenetisch, sondern auch ontogenetisch nach dem Verlust der Dentindecke entstehen, die Bildung der Dentindecke wäre während der Ontogenese unterdrückt worden.

Histologie (Abb. 14—16). Binokularmikroskopische Beobachtungen an den Resten und zahlreiche neue Schliffe geben die Möglichkeit zu Ergänzungen und Korrekturen an den Ausführungen, die ich 1956 gemacht habe. Wir wissen nun, daß es sich bei den 1956 noch fraglichen Resten um Bruchstücke der Schuppen und des Panzers eines Cephalaspiden, *Zenaspis* ? sp. indet. handelt. Auf den

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Resten finden sich nicht nur gelegentlich Dentintuberkel einer zweiten Generation, sondern in der Mehrzahl der Fälle regelrechte Dentindecken über den ontogenetisch primär angelegten Dentinleisten. Die Unterschicht dieser Reste wird von wunderbar regelmäßigem Isopedin (*isp*) aufgebaut, wie es für die Cephalaspiden charakteristisch ist (Abb. 14 B, 15 B und C). Den Acanthodiern (*Poracanthodes*) kommt demnach kein Isopedin zu; alle Beziehungen zu Acanthodiern fehlen.

Einen hervorragend gefärbten Schliff (Nr 899) habe ich 1956 in der Abb. 99 wiedergegeben unter Fortlassung der Pulpakanäle und Dentinröhrchen. Auf Grund der neuen Erfahrungen kann ich die genannte Abbildung dahin ergänzen, daß die primären Dentinleisten (*de.tub*) sich noch weiter, zum Teil unter den kleinen Maschenkanälen (Bildmitte, unten), ausdehnen, die gestreckten Vertiefungen zwischen den großen Maschenkanälen (*gr.m.k*) gänzlich erfüllend. In der Abbildung sind nicht die tiefer gelegenen Sockel der Dentinleisten, sondern nur die hochgelegenen Kämme wiedergegeben.

Wir können die großen Maschenkanäle (*gr.m.k*) jetzt als Circumarealkanäle (*cik*) und die kleinen Maschenkanäle (*kl.m.k*) als Intraarealkanäle (*iak*) bezeichnen. Die großen Maschen, die von den Circumarealkanälen gebildet werden, folgen in ihrer Anordnung den primären Dentinleisten (dnl_1), das Netzwerk des Porenkanalsystems hat daher in die Länge verzogene Maschen. Derselben Anordnung folgen auch weitgehend die Intraarealkanäle, nur weniger regelmäßig. Das Porenkanalsystem, insbesondere die Circumarealkanäle, liegen während der Bildung der primären Dentinleisten im Weichgewebe zwishen den Leisten. Durch die Bildung des sekundären Dentins werden alle Kanäle des Porenkanalsystems von Dentin umgeben und treten dadurch an den fossilen Resten sichtbar hervor. Die Lage der Circumareal- und der Intraarealkanäle läßt sich besonders gut in Horizontalschliffen verfolgen. Meist befindet sich zwischen den primären Dentinleisten nur ein Circumarealkanal, der entweder eine einzige mittlere Reihe großer Porenkanäle abgibt (Abb. 13 J) oder zwei Reihen etwas engerer Porenkanäle, die einander gegenüber stehen oder alternieren können (Abb. 13 E; 17 F). Seltener finden sich zwischen den primären Dentinleisten zwei parallel verlaufende Circumarealkanäle, die meist nur kurze Schlingen (Abb. 17 G) bilden und danach sich wieder vereinigen. In diesen Schlingen erheben sich niedrige primäre Dentintuberkel (Abb. 16 D) oder senken sich breite Pfeiler des sekundären Dentins herunter, um das sekundäre Dentin zwischen den primären Dentinleisten besser zu stützen (Abb. 17 C). Die Circumarealkanäle sind reichlich mit den Gefäßkanälen oder Gefäßkanalnetzen unter den primären Dentinleisten, aus denen die Pulpakanäle dieser Leisten entspringen, durch enge Querkanäle verbunden (Gross 1956, Abb. 110 C und 104; ferner in den Abb. 14 und 15 der vorliegenden Schrift).

Aus den Seiten der Circumarealkanäle erheben sich schräg nach oben die viel

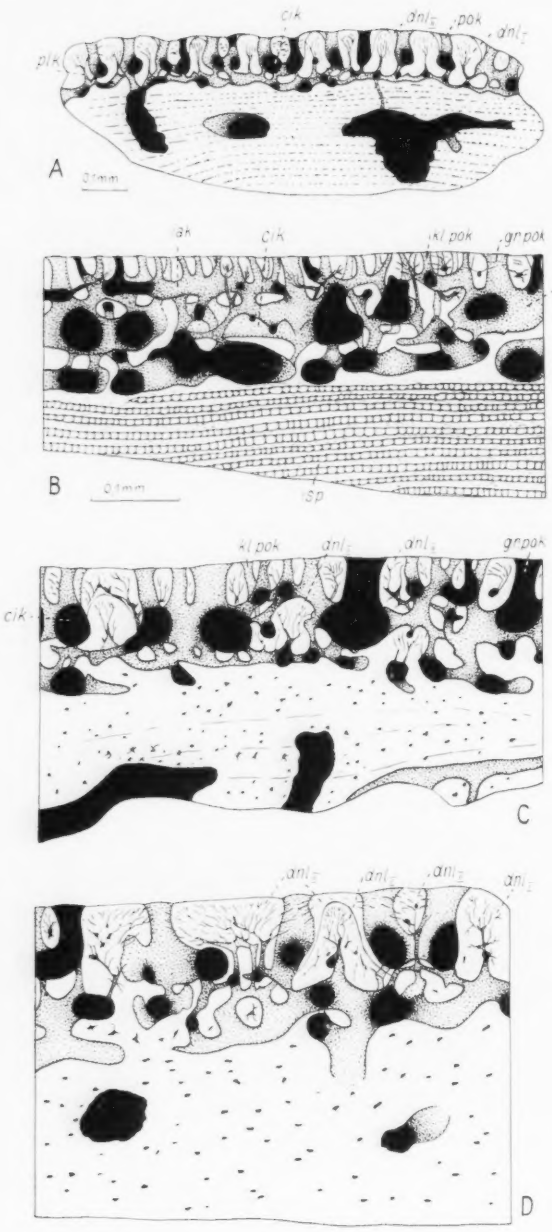

Abb. 14. *Zenaspis* ? sp. indet. Dünnschliffe. A Schliff Nr. 2205 Berlin; vertikaler Querschliff durch eine Schuppe mit geringer sekundärer Dentinbildung; × 65. B Schliff Nr. 2225 Berlin; vertikaler Längsschliff parallel zu einem Circumarealkanal; Circumareal- und Intraarealkanäle deutlich verschieden; ausgeprägtes Isopedin; × 125. C Schliff Nr. 2218 Berlin; vertikaler Querschliff durch Rest mit dicker sekundärer Dentindecke, Circum- und Intraarealkanälen; × 125. D Schliff Nr. 2219 Berlin; vertikaler Querschliff durch Rest mit überdeckten primären Dentinleisten und breiten sekundären Dentinleisten; × 125. *cik* Circumarealkanal; *dnl*$_{I-II}$ primäre und sekundäre Dentinleisten; *gr.pok* große Porenkanäle der Circumarealkanäle; *iak* Intraarealkanäle; isp Isopedin; *kl.pok* kleine Porenkanäle der Intraarealkanäle; *plk* Pulpakanäle.

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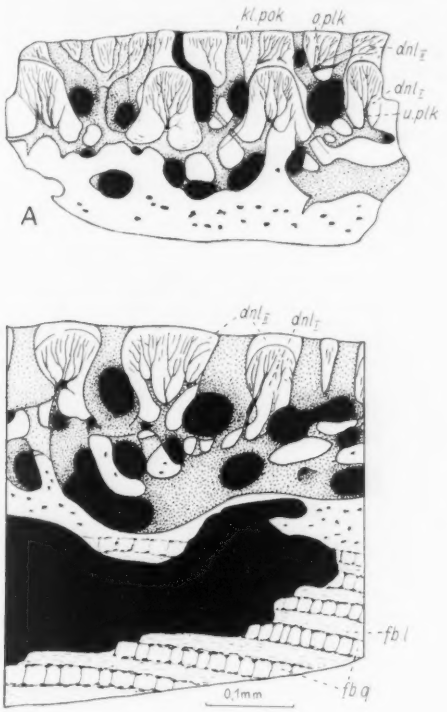

Abb. 15. *Zenaspis?* sp. indet. Dünnschliffe; × 125. A Schliff Nr. 2215 Berlin; vertikaler Querschliff durch Schuppe mit sekundärer Dentindecke über primären Dentinleisten. B Schliff Nr. 2207 Berlin; vertikaler Querschliff durch Rest mit dünner sekundärer Dentindecke und breiten sekundären Dentinleisten. C Schliff Nr. 2213 Berlin; vertikaler Längsschliff parallel zu primärer Dentinleiste und Intraarealkanal, so daß überwiegend sekundäres Dentin sichtbar ist; Isopedin mit größeren Hohlräumen. dnl_{I-II} primäre und sekundäre Dentinleisten; *fb.l* längsgetroffene Faserbündel des Isopedins; *fb.q* quergetroffene Faserbündel des Isopedins; *kl.pok* kleine Porenkanäle der Intraarealkanäle; *o.plk* Pulpakanäle in sekundärer Dentinleiste; *plx* Plexus der Arkadenkanäle in sekundärer Dentinleiste; *u.plk* Pulpakanal in primärer Dentinleiste.

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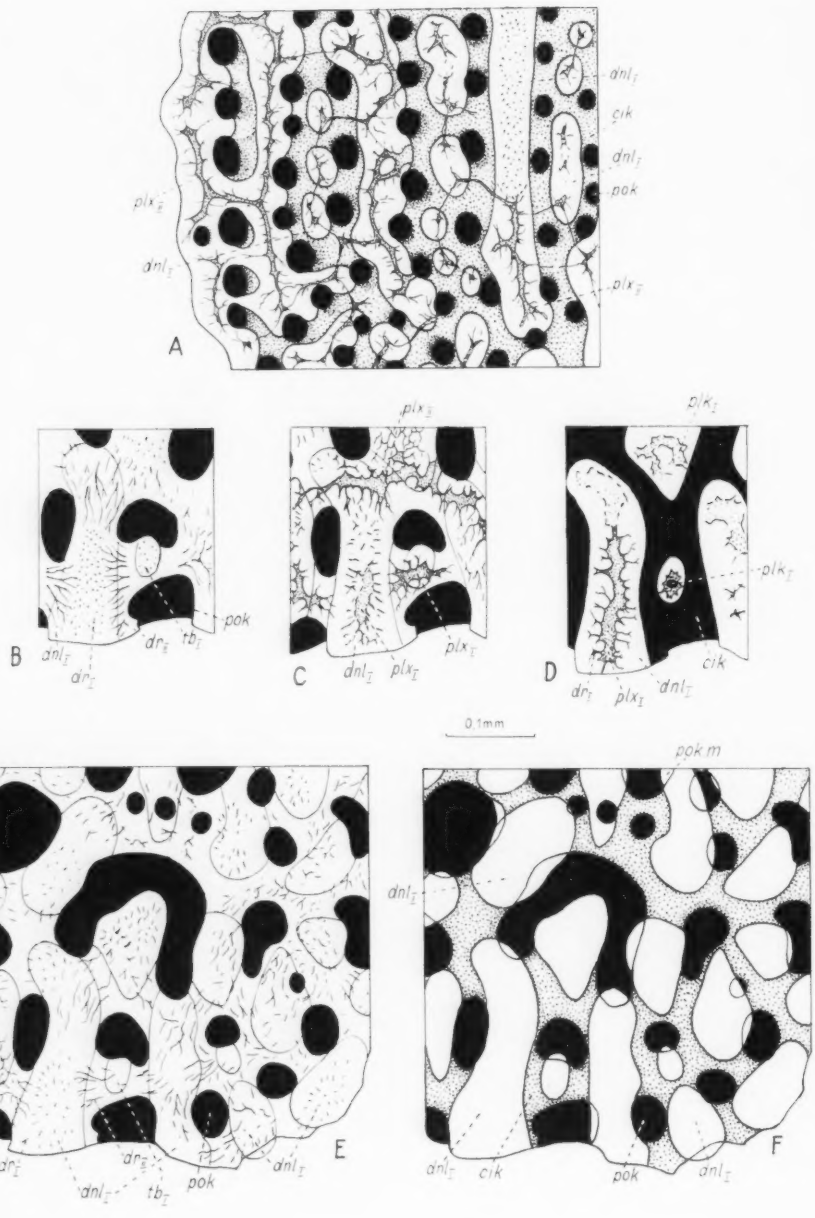
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engeren Intraarealkanäle (*iak*), die entsprechend engere und kürzere Porenkanäle (*kl.pok*) entsenden. Meist begleiten die Intraarealkanäle die Circumarealkanäle bzw. die primären Dentinleisten girlandenförmig (Gross 1956 Abb. 99 und 104), aber sie können auch über den primären Dentinleisten ein Netzwerk bilden (Abb. 14 B und C). Oft aber greifen nur die kleinen Porenkanäle seitlich über die primären Dentinleisten (Abb. 15 A). Selbst in vertikalen Längsschliffen ist die Lagebeziehung der Circumarealkanäle zu den Intraarealkanälen manchmal gut zu erkennen (Abb. 14 B). Die Intraarealkanäle werden nicht von Blutgefäßkanälen der Mittelschicht versorgt, sie stehen nur mit den Circumarealkanälen in Verbindung. In manchen Resten kommt es nicht zur Entwicklung von gesonderten Circum- und Intraarealkanälen, sondern es besteht zwischen den primären Dentinleisten nur ein Circumarealkanalnetz aus engen Kanälen (Abb. 14 A und 15 C), deren Durchmesser nicht viel weiter ist als der der Intraarealkanäle anderer Reste mit großen Circumarealkanälen. Schon oberflächlich läßt sich das Vorhandensein nur enger Circumarealkanäle an den gleichmäßig engen Mündungen der Porenkanäle erkennen. An ein und demselben Rest kann ein Wechsel in der Ausbildung der Porenkanalsystems schon auf kürzeste Entfernung eintreten. Je dicker die sekundäre Dentindecke ist, um so mehr hat das System der Intraarealkanäle Platz zur Ausbreitung. — Zeigen die Porenkanäle eine bemerkenswerte Verbiegung nach einer bestimmten Seite (Abb. 14 B), so kann man danach die Reste orientieren: die Krümmungen weisen stets nach hinten, nicht anders als im Dentin der Schuppen von *Dipterus* (Gross 1956 Abb. 70 A).

Die Pulpakanäle (*plk*) des primären und des sekundären Dentins entspringen stets den Gefäßkanälen der Mittelschicht. Die Pulpakanäle der primären Dentinleisten erheben sich nicht selten von ziemlich gerade unter den Dentinleisten verlaufenden Längskanälen, die ich 1956 (Abb. 104) als Pulpasammelkanäle bezeichnet habe. Diese Kanäle liegen meist merklich tiefer als die Circumarealkanäle. Werden die primären Dentinleisten sehr breit, so entwickelt sich unter ihnen statt der geraden Pulpasammelkanäle ein unregelmäßiges horizontales Netz von

Abb. 16. *Zenaspis* ? sp. indet. Horizontalschliffe durch die Oberschicht; × 125. A Schliff Nr. 2235 Berlin; Horizontalschliff durch die Oberschicht mit Circumarealkanälen und überwiegend sekundärem Dentin mit Gefäßplexus zwischen den Porenkanälen. B—D Schliff Nr. 2240 Berlin; Ausschnitt aus Horizontalschliff durch die Oberschicht bei von oben nach unten (B—D) wechselnder Einstellung. B zeigt Dentinröhrchen des sekundären Dentins. C zeigt die darunter liegenden Plexus des sekundären und primären Dentins. D zeigt primäre Dentinleisten und die Circumarealkanäle bezw. Zwischenfurchen. E—F Schliff Nr. 2240 Berlin; Horizontalschliff durch die Oberschicht; enthält die Ausschnitte Fig. B—D; E Einstellung auf die sekundäre Dentinschicht. F Einstellung auf die Circumarealkanäle bezw. Zwischenfurchen und die Basis der primären Dentinleisten. *cik* Circumarealkanal; dnl_{I-II} primäre und sekundäre Dentinleisten; dr_{I-II} Dentinröhrchen des primären und sekundären Dentins; plk_I Pulpakanal des primären Dentins; plx_{I-II} Gefäßplexus der Arkadenkanäle im primären und sekundären Dentin; *pok* Porenkanal; *pok.m* Mündung des Porenkanals; tb_I primärer Dentintuberkel in Schlinge des Circumarealkanals.

Kanälen, aus denen sich die Pulpakanäle erheben. Kurze primäre Dentintuberkel (Abb. 16 D) haben oft nur einen einzigen Pulpakanal.

Die Pulpakanäle des sekundären Dentins entspringen meist etwas höher, überwiegend aus den queren Verbindungskanälen zwischen dem Pulpasammelkanal und den Circumarealkanälen (Gross 1956 Abb. 104). Manchmal bilden sich parallel zu den Circumarealkanälen und ihnen dicht anliegend Längsgefäße, die in regelmäßigen Abständen die Pulpakanäle des sekundären Dentins entsenden, und zwar in dem engen Raum zwischen der Seitenwand der primären Dentinleiste und dem Circumarealkanal (Abb. 17 D und E).

Die Pulpakanäle der primären Dentinleisten verbinden sich mit ihren Oberenden untereinander durch enge Arkadenkanäle, die einen engmaschigen Plexus (plx_I) bilden, aus dem ebenso wie aus den Enden der Pulpakanäle die Dentinröhrchen strahlen (Abb. 16 C und D). Die Dentinröhrchen sind überwiegend nach oben gerichtet, in den Enden der Dentinleisten werden sie besonders lang und verlaufen mehr horizontal (Gross 1956 Abb. 101 B). Viel ausgeprägter ist die Plexusbildung im sekundären Dentin (Abb. 16 A, plx_{II}), die eine Ausrichtung nach den Porenkanälen erfährt. Die Porenkanäle werden maschenförmig umfaßt. Oft kann man den Plexus des sekundären Dentins dicht über den Enden der Dentinröhrchen der primären Dentinleisten erkennen (Abb. 16 A, rechts unten). Auch in Vertikalschliffen sind die arkadenförmigen Verbindungen der Pulpakanäle des sekundären Dentins über und zwischen den primären Dentinleisten gut zu sehen (Abb. 14 B und C, 15 A und C). Die Dentinröhrchen des sekundären Dentins (dr_{II}) verlaufen vielfach horizontal, namentlich wenn die sekundäre Dentindecke dünn ist (Abb. 14 D, 15 C, 16 B und E). Dabei bilden sie oft ausgedehnte Netze (Gross 1956 Abb. 101 A), in die nicht selten etwas tiefer zellenartige Lakunen eingeschaltet sind. Meist kann man das primäre Dentin vom sekundären an der Ausbildung der Dentinröhrchen unterscheiden. Nie verbinden sich die Dentinröhrchen beider Dentingenerationen.

In dicken Horizontalschliffen erscheinen die primären Dentinleisten — von oben betrachtet — viel schmaler und kürzer als bei einer Betrachtung von unten (dünne Objektträger gestatten noch bei stärkerer Vergrößerung eine mikroskopische Beobachtung von der Unterseite), da ihre Seitenflächen von dem Intraarealkanalsystem vielfach verdeckt werden. Sind ausgeprägte Circumarealkanalmaschen entwickelt, so kann man mit Sicherheit voraussetzen, daß sie von primären Dentinleisten oder primären Dentintuberkeln eingenommen werden (vgl. Bemerkung auf S. 117).

Nicht immer sind auf den Vertikalschliffen primäre und sekundäre Dentingebilde leicht zu unterscheiden, da sich das sekundäre Dentin in breiten und tiefen Furchen zwischen den primären Dentinleisten auf den Boden der Furchen stützt und damit in gleicher Höhe ansetzt wie die primären Dentinleisten. Nur reicht das sekundäre Dentin vielfach höher als das primäre und stößt an letzteres mit einer ausgeprägten Grenzlinie (Abb. 14 D). In der Abb. 15 B sehen wir ebenfalls

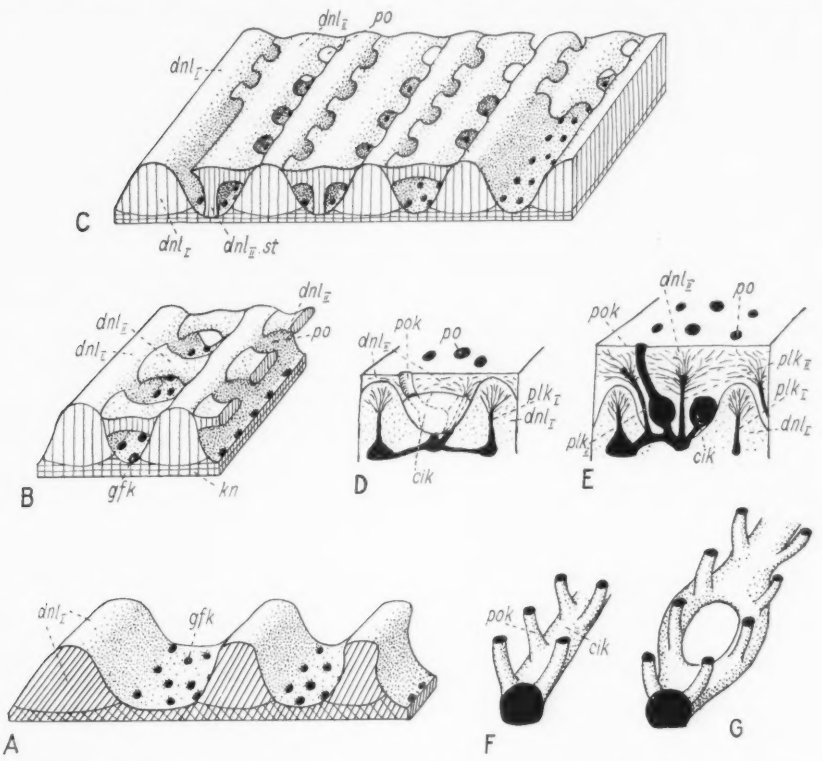

Abb. 17. *Zenaspis* ? sp. indet. Schematische Abbildungen zur Darstellung der Dentinbildung und der Circumarealkanäle. A verschiedene Ausbildung der primären Dentinleisten und ihrer Zwischenfurchen. B Bildung sekundären Dentins in Gestalt von Quersprossen zwischen den primären Dentinleisten. C Bildung sekundärer Dentinleisten und Dentinbrücken zwischen primären Dentinleisten. D Bildung dünner sekundärer Dentindecke. E abgeschlossene Bildung einer dicken sekundären Dentindecke. F Circumarealkanal mit Doppelreihe von Porenkanälen seitlich der sekundären Dentinleiste. G Circumarealkanal mit Schlingenbildung um primären Dentintuberkel bezw. -Pfeiler. *cik* Circumarealkanal; dnl_{I-II} primäre und sekundäre Dentinleisten; $dnl_{II}st$ Stütze der sekundären Dentinleiste; *gfk* Gefäßkanal; plk_{I-II} Pulpakanäle des primären und sekundären Dentins; *po* Mündung des Porenkanals; *pok* Porenkanal.

eine sekundäre Dentinleiste zwischen zwei primären Dentinleisten, die schmaler und niedriger sind. Vielfach erkennt man nur Teile der auf die primären Dentinleisten aufgelagerten Quersprossen des sekundären Dentins (dnl_{II}) als schmale Streifen an den Flanken der primären Dentinleisten (Abb. 14 A und D, 15 B). Während der Bildung des sekundären Dentins überdacht es oft nur in dünner Schicht die Furchen zwischen den primären Dentinleisten (Abb. 17 C, rechts). Von solchen Stadien habe ich keine guten Querschliffe, aber einen sehr schönen Horizontalschliff. Betrachtet man diesen Schliff von unten, so sieht man die wei-

ten, jetzt leer erscheinenden Zwischenfurchen von einer durchgehenden dünnen Decke sekundären Dentins überdacht. Das Dentin ist gegen das primäre Dentin, an das es vielfach grenzt, durch feine Linien und die eigenen Dentinröhrchen deutlich abgegrenzt. Da die Decke sehr dünn ist, enthält sie nur die Dentinröhrchen, aber noch keinen Arkadenplexus und keine Pulpakanäle. Diese Kanäle lagen noch im Weichgewebe unter der sich bildenden Dentindecke (Abb. 17 D). Wäre der Dentinbildungsprozeß durch den Tod des Tieres nicht zum Abbruch gekommen, so würden die Arkaden- und Pulpakanäle vom Dentin bis auf den Boden der Zwischenfurche oder bis an die Circumarealkanäle eingeschlossen sein. So zeigen auch manche Schliffe dasselbe Bild, das man leichter an Bruchflächen der Schuppen mit der binokularen Lupe sehen kann, wenn auch ohne histologische Einzelheiten, da die Vergrößerung zu gering ist. Die von Weichgewebe erfüllten Hohlräume unter der sich bildenden sekundären Dentindecke waren sehr wahrscheinlich nicht von einer Art Pulpa erfüllt, sondern nur von den Pulpakanälen und dem sie umgebenden, noch kolloidalen Dentin. Bei diesen kleinen Gebilden kann man nicht erwarten, daß das Dentin von einer sich zurückziehenden Schicht von Odontoblasten gebildet wurde, etwa nach Art der Bildungsweise größerer Mundzähne.

Die Mittelschicht der *Zenaspis?*-Reste ist meist nur gering entwickelt. Sie steht in engster Verbindung mit der Dentinbildung, indem sie die Pulpakanäle entsendet und die Circumarealkanäle mit Gefäßkanälen versorgt. Tesserae mit typischen Radiärkanälen habe ich bisher nur in einigen, schlecht erhaltenen Resten gefunden, von denen nicht gesagt werden kann, daß sie zu *Zenaspis* ? gehören. Einige *Zenaspis* ?-Reste zeigen stellenweise eine auffallend regelmäßig parallele Anordnung von Spongiosakanälen quer zu den primären Dentinleisten. Es kann leider nicht festgestellt werden, von welcher Stelle des Panzers diese Bruchstücke stammen.

In manchen Vertikalschliffen sieht man aufsteigende enge Spongiosakanäle, etwa am Rande der primären Dentinleiste, die sich aufgabeln. Ein Ast zieht als Pulpakanal in die primäre Dentinleiste, der andere als Pulpakanal in das sekundäre Dentin der Zwischenfurche. Die zahlreichen Gefäßkanalmündungen am Boden der Zwischenfurchen (Abb. 13 E, G und H) gaben sowohl den Gefäßkanälen den Durchtritt, die die Circumarealkanäle versorgten, wie auch den Pulpakanälen des sekundären Dentins (Abb. 17 E). Fehlt das sekundäre Dentin, so kann man nur aus ihrer Lage in der Zwischenfurche die Aufgabe der Kanalmündungen erschließen.

Die Unterschicht ist als typisches Isopedin (*isp*) entwickelt (Abb. 14 B, 15 B und C), in welchem sich weite Hohlräume ohne eigene lamelläre Umwandung befinden.

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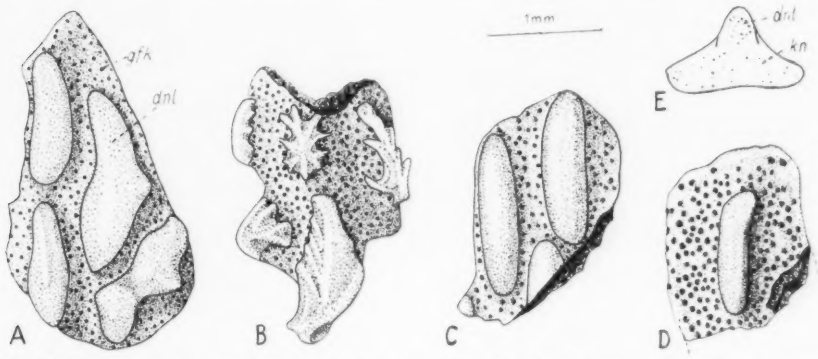

Abb. 18. Osteostraci: genus indeterminabile; × 16. A Bruchstück mit groben Dentinleisten; f 689. B Bruchstück mit kleineren gezackten Dentinleisten; f 690. C Bruchstück mit typischen glatten Dentinleisten; f 691. D Tesseraartiges Bruchstück mit einfacher glatter Dentinleiste; f 692. E Querschnitt durch den in Fig. D wiedergegebenen Rest. *dnl* Dentinleiste auf breitem Knochensockel; *gfk* Gefäßkanal; *kn* Knochensockel der Dentinleiste.

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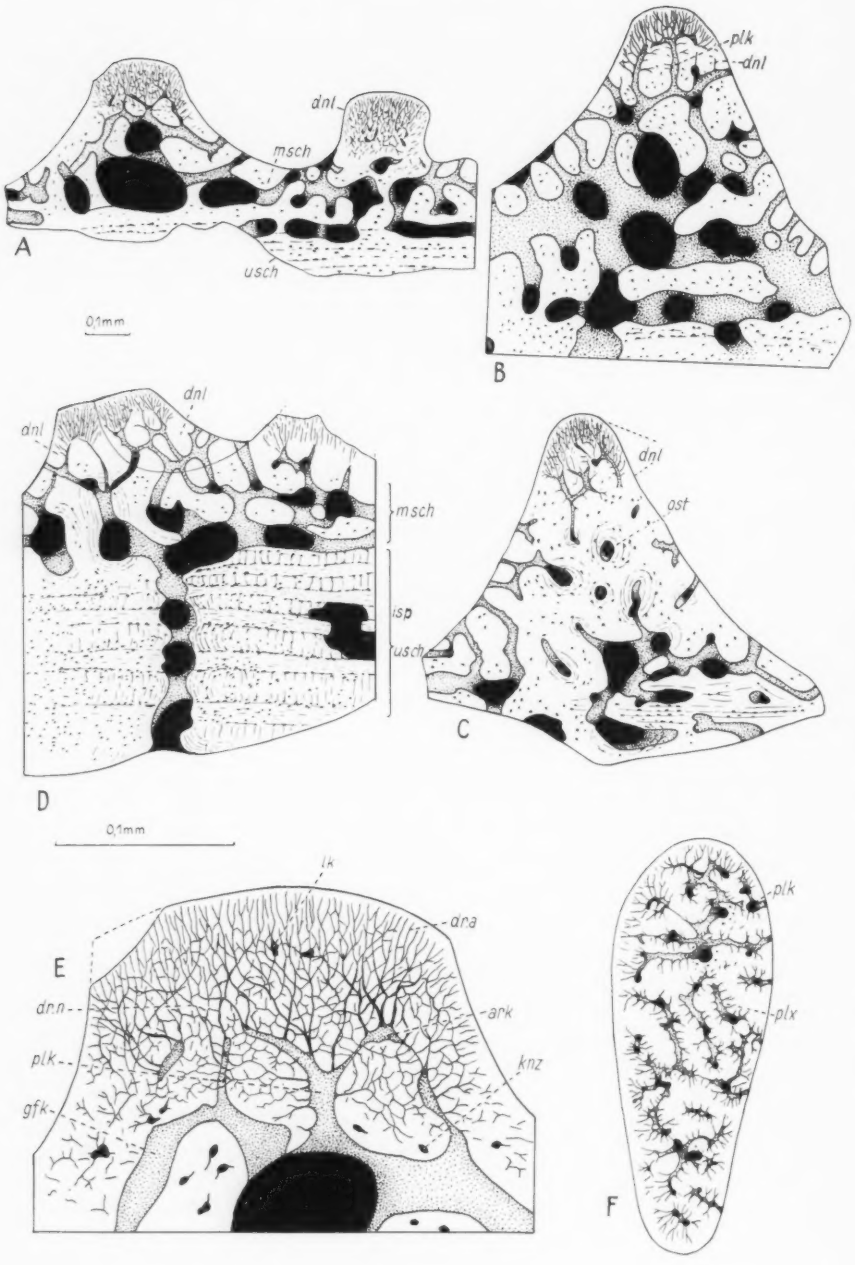
OSTEOSTRACI: GENUS INDETERMINABILE

In den Geschieben Bey. 36 und 37 finden sich recht zahlreich Bruchstücke eines Cephalaspiden-Panzers, die eine von *Zenaspis* ? sp. indet. abweichende Skulptur und einen andersartigen histologischen Aufbau haben. Ich glaube nicht, daß diese Reste von großen Individuen der Gattung *Zenaspis* ? stammen. Ich habe nur einen einzigen schlecht erhaltenen Rest mit mehreren Tesserae gefunden, alle übrigen Reste sind Bruchstücke, die keine natürliche Begrenzung zeigen.

Besonders charakteristisch ist die Skulptur (Abb. 18), die sich meist aus gestreckten und recht hohen Wällen ohne Seitenzacken zusammensetzt (Abb. 18 A, C, D). Andere Bruchstücke weisen zwischen den Wällen gelegentlich kleinere Tuberkel auf. Reste, die anscheinend von den Seitenrändern des Kopfschildes stammen, sind mit gezackten Skulpturen wechselnder Größe besetzt (Abb. 18 B), deren Seitenzacken ein wenig nach vorne gerichtet sind. Ähnlich gestaltete Tuberkel zeigt ein von Wills (Taf. 4 Fig. 2) abgebildeter Rest. Die Skulpturen heben sich durch ihre matt schimmernde gelbliche oder weißliche Farbe sehr deutlich vom rötlichen Knochen ab. Die Skulpturen sind meist doppelt so breit und hoch wie die Skulpturen von *Zenaspis* ? sp. indet. Kein Rest hat sekundäre Dentinbildungen zwischen den Wällen. Der Abstand der Wälle ist sehr verschieden. In den Vertiefungen zwischen den Wällen münden zahlreiche Gefäßkanäle auf der Oberfläche des Knochens. Der Durchmesser der Mündungen beträgt etwa 25 μ. Die Skulptur-Wälle bestehen aus einem breiten Knochensockel, der von Dentin gekrönt wird (Abb. 18 A, C und E). Die schräg abfallenden Seitenflächen der Skulpturen bestehen oben aus Dentin, unten aus Knochen. Das Dentin ist dicht, der Knochensockel wird jedoch von zahlreichen, seitlich mündenden Gefäßkanälen durchbohrt. Dieser deutlich in die Skulptur einbezogene Knochen-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sockel fehlt bei *Zenaspis* ? sp. indet. Der Anteil beider Gewebearten an den Skulpturen wechselt ungemein. Auf den schlecht erhaltenen Tesserae sind die Skulpturen kurz und flach tuberkelfömig. Der in der Abb. 18 D wiedergegebene Rest ist ein einziger breiter Knochensockel mit einer relativ schmalen Dentinleiste als Krönung (vgl. den Querschnitt, Abb. 18 E). Kein Rest zeigt Andeutungen des Porenkanalsystems, das sich vermutlich in der Haut zwischen den Skulpturen ausbreitete. Die Skulpturwälle sind oft 1 bis 1,5 mm lang und werden 200—450 μ breit.

Histologie (Abb. 19 und 20). Die relative Spärlichkeit des Materials erlaubt leider nicht, so zahlreiche Schliffe herzustellen, wie es wünschenswert wäre. Vielleicht würde sich bei einer größeren Anzahl von Schliffen doch gelegentlich Dentin in zwei Bildungsgeneration nachweisen lassen, etwa kleinere Dentintuberkel unter der obersten Knochenschicht. Aneinanderlagerung von zwei Skulpturwällen zeigt die Abb. 19 D; aus gemeinsamen Blutgefäßkanalnetz bilden sich Dentinleisten (*dnl*), die nur durch eine Trennungslinie gesondert bleiben.

Der Dentinmantel der Skulpturen besetzt oft nur das obere Drittel der Skulpturen (Abb. 19 B und C), der mächtige Sockel besteht aus Knochengewebe. Das Dentin wird von senkrecht oder schräg aufsteigenden engen Pulpakanälen gebildet, die sich an ihren oberen Enden arkadenförmig verbinden und dadurch einen unregelmäßigen Plexus bilden (Abb. 19 F, Abb. 20), aus dem zahlreiche Zellausläufer bzw. Dentinröhrchen strahlen, die untereinander netzartig verbunden sind (Abb. 19 E, 20 A). Nicht selten schwellen die Ausläufer lakunenartig an (Abb. 19 E). Besonders schön ausgeprägt kann das Netzwerk der Ausläufer (*dr.n*) zwischen den Pulpakanälen unterhalb des Plexus sein (Abb. 20 B). Nach unten geht das Netzwerk ohne scharfe Grenze in das weniger regelmäßige Netzwerk der Ausläufer der Knochenzellen über, es erscheinen nun zahlreich auch die Knochenzellen. Die aus dem Plexus strahlenden Dentinröhrchen (*dr.a*) verlaufen regelmäßig parallel zueinander, wenn auch stets aufs reichlichste durch Querästchen verbunden. Die Querverbindungen reichen oft bis dicht unter die Oberfläche des Dentinmantels, doch enden die Ausläufer frei. Diese Art des Dentins ist typisch für Osteostraci; in den größeren Skulpturen ist es besonders charak-

Abb. 19. Osteostraci: genus indeterminabile; Dünnschliffe. A Schliff Nr. 2260 Berlin; vertikaler Querschliff durch zwei Dentinleisten; × 65. B Schliff Nr. 2262 Berlin; vertikaler Querschliff durch Dentinleiste und ihren Knochensockel; × 65. C Schliff Nr. 2256; vertikaler Querschliff durch Dentinleiste und ihren Knochensockel; × 65. D Schliff Nr. 2261; vertikaler Querschliff durch Bruchstück mit Dentinleisten; zwei Dentinleisten lagern sich aneinander (links); Isopedin und aufsteigendes Gefäß; × 65. E Schliff Nr. 2260 Mesodentin der Dentinleiste (vgl. Fig. A, links); × 255. F Schliff Nr. 2265 Berlin; Horizontalschliff durch Dentinleiste in der Höhe des Plexus; × 65. *ark* Arkadenkanal; *dnl* Dentinleiste; *dr.a* Ausläufer der Dentinröhrchen; *dr.n* Netzwerk der Dentinröhrchen; *gfk* Gefäßkanal; *isp* Isopedin; *lk* Lakunen des Mesodentins; *knz* Lakunen der Knochenzellen; *msch* Mittelschicht; *ost* primäres Osteon; *plk* Pulpakanal; *plx* Plexus der Arkadenkanäle unter den Dentinröhrchen; *usch* Unterschicht.

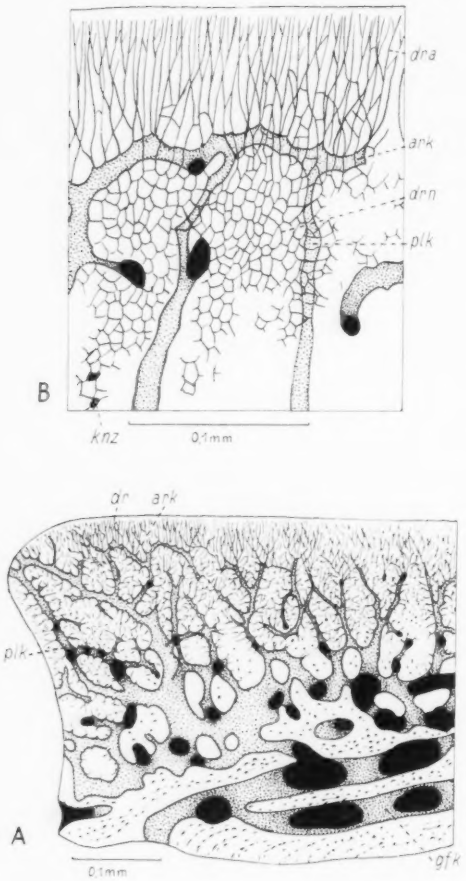

Abb. 20. Osteostraci: genus indeterminabile. Dünnschliffe zur Veranschaulichung det Mesodentins. A Schliff Nr. 2236 Berlin; vertikaler Längsschliff durch Dentinleiste; × 65. B Schliff Nr. 2264 Berlin; Mesodentin mit Pulpakanälen, Arkadenkanälen und Dentinröhrchennetz; × 225 *ark* Arkadenkanal; *dr* Dentinröhrchen; *dr.a* Ausläufer der Dentinröhrchen; *dr.n* netzartige Verbindung der Dentinröhrchen; *gfk* Gefäßkanal; *knz* Lakune der Knochenzellen; *plk* Pulpakanal.

teristisch ausgebildet. Für diese Dentinart der Osteostraci und der Acanthodier des *Nostolepis*-Typus hat Ørvig die Bezeichnung Mesodentin geprägt, um damit die Mittelstellung zwischen Orthodentin und Knochengewebe anzudeuten.

Im knöchernen Sockel der Skulpturen gehen die Pulpakanäle in ein grobes Netz überwiegend horizontal und quer zur Längsrichtung der Wälle verlaufender Gefäßkanäle über, die an relativ wenigen Stellen von breiteren, aus der Mittelschicht aufsteigenden Gefäßkanälen versorgt werden. Die Gefäßkanäle im Sockel der Skulpturen sind oft von sehr ausgeprägten primären Osteonen (*ost*) umgeben (Abb. 19 C), die auch in der spongiösen Mittelschicht reichlich zu finden sind. Die Mittelschicht ist stärker entwickelt als bei *Zenapis* ? sp. indet.; ihre aufsteigenden Gefäßkanäle münden auf der Oberfläche zwischen den Skulpturen. Auch aus den Sockeln der Skulpturen treten viele engere Gefäßkanäle seitlich und radial aus (Abb. 19 B und C).

Die Unterschicht ist meist als typisches Isopedin entwickelt (Abb. 19 D), das von relativ wenigen aufsteigenden Gefäßkanälen durchbohrt wird, die sich mit keinen primären Osteonen umwanden. Die einzelnen Lagen des Isopedins können recht dick werden, so daß in ihnen manchmal gleichgerichtete Faserbündel in zwei Schichten zu finden sind.

Die Trabekeln der Mittelschicht eines nicht abgebildeten Schliffes sind völlig globulär gebaut. Der Durchmesser der Kugeln entspricht etwa der der Lakunen der Knochenzellen. Vermutlich ist hier in Bildung begriffenes Knochengewebe getroffen, dessen Umwandlung in lamellären Knochen man sich nicht recht vorstellen kann. Das Mesodentin über den Knochen zeigt keinen globulären Aufbau.

Das Mesodentin der primären Dentinleisten von *Zenaspis* ? sp. indet. ist orthodentinartiger als das der eben beschriebenen unbestimmten Gattung. Am Aufbau des Dentins sind beide Gattungen leicht zu unterscheiden.

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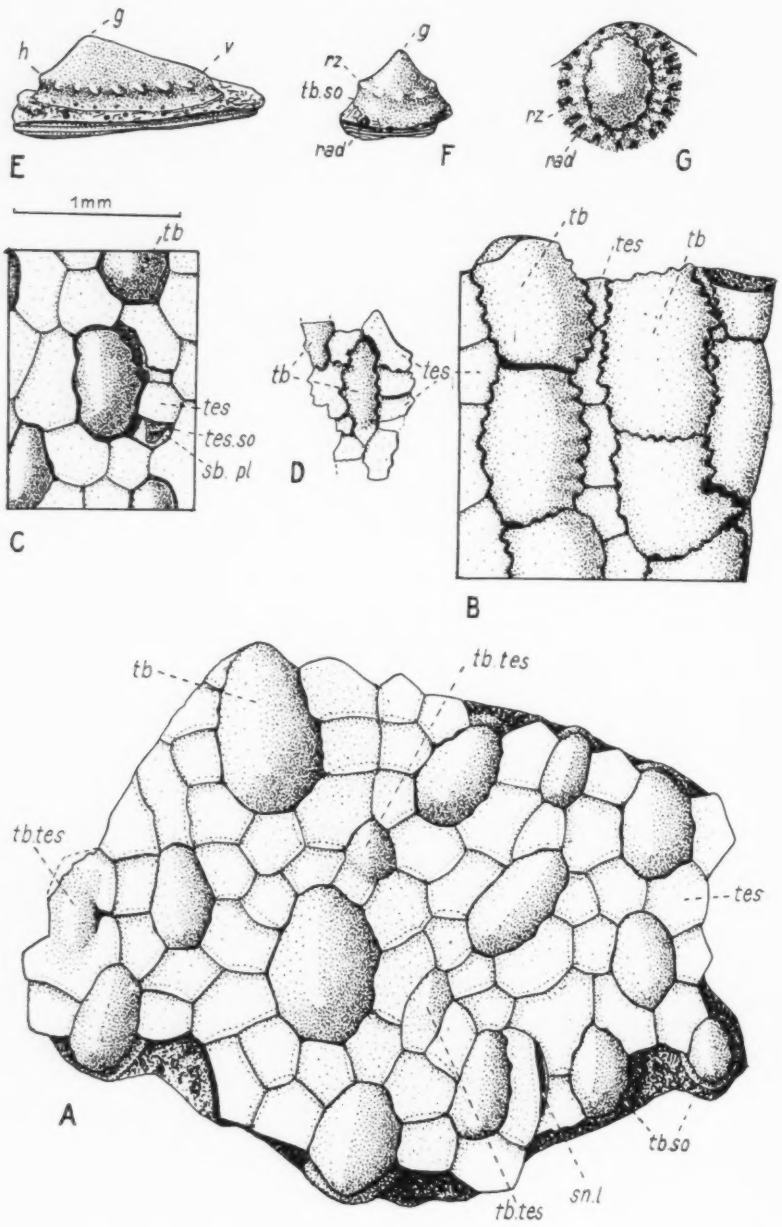
DARTMUTHIA GEMMIFERA PATTEN

Nachdem ich 1956 ausführlich das Porenkanalsystem und die merkwürdigen Siebplatten von *Trematapis* beschrieben hatte, regte sich in mir der Wunsch, den Befund an *Trematapis* mit den Verhältnissen bei der Gattung *Dartmuthia* zu vergleichen, die nach den Angaben von Denison (1951 b) und Bölau (1951) ebenfalls Siebplatten besitzt. Mir stand nur wenig Material zur Verfügung, ein größerer, recht vollständiger Dorsalpanzer und zerstreute Bruchstücke eines Dorsalpanzers, die ich mit Essigsäure aus dem Gestein löste. Auf diese Weise gewonnene Reste eignen sich vielfach besonders gut zur Herstellung von Dünnschliffen. Die Untersuchung der verschiedenen Bruchstücke und der Schliffe brachte recht viele Ergänzungen zu den Beobachtungen der genannten Autoren.

Nach Denison (1951 b) ist der Ventralpanzer glatt und skulpturlos, die oberste Lage der knöchernen Oberschicht hat den Charakter von Mesodentin. Die Oberfläche des Dorsalpanzers setzt sich dagegen aus zahlreichen verstreuten oder auch in geraden Längsreihen angeordneten ovalen Tuberkeln und niedrigen polygonalen Tesserae zusammen. Die Tuberkel sind matt tiefbraun gefärbt und überragen die spiegelglatten, ebenen, fast weißlichen Tesserae. Auch die Seitenränder sind mit einer Tuberkelreihe verziert, deren Tuberkel unmittelbar einander folgen, nur durch schmale, im Zickzack verlaufende Furchen getrennt (Abb. 21 B, rechts). Die Furchen zwischen den Randtuberkeln entsprechen vermutlich den Furchen zwischen den polygonalen Feldern, in die der Ventralpanzer zerlegt ist (Denison 1951 b, Fig. 34 B). Die Furchen sind die spaltförmigen Mündungen der Maschenkanäle (Circumarealkanäle) des Porenkanalsystems. Der Ventralpanzer von *Dartmuthia* ist ebenso wie der von *Trematapis* gleichmäßig von einer dichten Oberschicht bedeckt, die das Porenkanalsystem einschließt. Bei *Trematapis* münden die Maschenkanäle durch Porenkanäle, bei *Dartmuthia* durch Spalten, die vielleicht durch seitliche Vereinigungen der Porenkanäle zustandegekommen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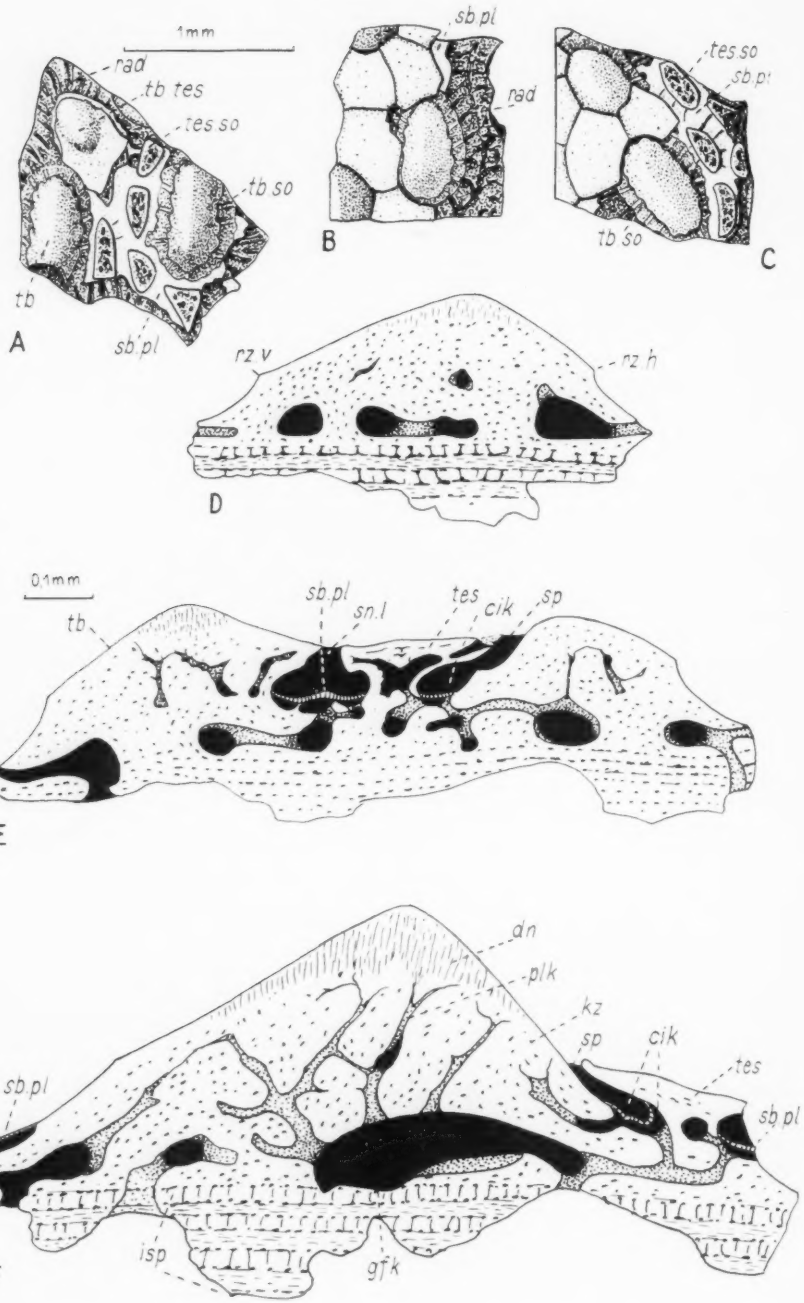
sind. Bei beiden Gattungen besteht die Oberschicht aus Knochengewebe, das nach oben hin den Charakter von Mesodentin annimmt, bei *Trematapis* in den wenigen Tuberkeln besonders ausgeprägt. Das in Knochen gebettete Porenkanalsystem dieser beiden Gattungen ist daher unabhängig von „Hautzahnbildungen", wie sie für die Osteolepiden, *Porolepis* und die Dipteriden charakteristisch sind. Aber auch bei den eben genannten Gattungen und Familien der Osteichthyes dürfte das Porenkanalsystem grundsätzlich unabhängig von den Dentinbildungen der Oberschicht sein, wenn es auch stets von diesen überlagert und eingeschlossen wird. Der Schutz des Porenkanalsystems durch Einschluß in die Oberschicht ist nicht unbedingt an die Bildung von Dentin oder Hautzähnen bzw. Lepidomorien gebunden, wie uns die beiden Gattungen *Trematapis* und *Dartmuthia* zeigen.

Die Tuberkel des Dorsalpanzers von *Dartmuthia* (Abb. 21 u. 22) sind überwiegend länglich ovale Gebilde, die am Hinterende einen Gipfel (*g*) aufweisen und nach vorne schräg abfallen. Das Hinterende der meisten Tuberkel ist breiter als das Vorderende, doch kommen auch fast kreisrunde Tuberkel vor. Auf etwa halber Höhe ist der Tuberkel ringsum mit Randzacken versehen (*rz*), die oft deutlich nach vorne gewendet sind und dem Tuberkel einen eichenblattförmigen Umriß geben können (Abb. 22 A). Mit Hilfe dieser Merkmale lassen sich die meisten Bruchstücke des Dorsal-Panzers orientieren, da — abgesehen vom Vorderende des Panzers — die Längsrichtung der Tuberkel mit der Längsrichtung des Panzers zusammenfällt. Unterhalb der Randzacken ist die Seitenwand des Tuberkels glatt und schräg abfallend, oft sogar im Profil etwas konkav (Abb. 21 E und F, Abb. 22 D, 23 A). Dieser untere Teil des Tuberkels sei als Tuberkelsockel (*tb.so*) bezeichnet.

Die Tuberkel sind stets tiefbraun gefärbt. Auch im Schliff erscheint der Tuberkel tiefbraun, aber seine oberste Spitze wird hell weißlich, da in ihr das Knochengewebe in lichtdurchlässiges Mesodentin übergeht (Abb. 22 D—F).

Zwischen den Tuberkeln breiten sich die polygonalen Platten (intertubercular plates von Wängsjö, 1946) aus, die ich als Tesserae bezeichne (*tes*). Ihre Oberfläche ist spiegelglatt, durch ihre helle Farbe und den auffallenden Glanz heben sie sich scharf von den Tuberkeln ab. An die Tuberkel grenzen sie etwa

Abb. 21. *Dartmuthia gemmifera* Patten. Bruchstücke des Dorsalpanzers; × 25. A Bruchstück mit Tuberkeln, Tesserae und Übergängen zwischen beiden; Sinneslinie (rechts unten); f 693. B Bruchstück vom Seitenrand des Dorsalpanzers mit aneinanderschließenden Tuberkeln; f 694. C Bruchstück mit z.T. beschädigten Tesserae, so daß deren Sockel und die Siebplatten sichtbar werden; f 695. D randlicher Tuberkel, dessen Hinterende in Tessera übergeht; f 696. E Tuberkel von der rechten Seite; f 697. F. Tuberkel von hinten. G Tuberkel mit austretenden radiären Kanälen, von oben. *g* Gipfel des Tuberkels; *h* Hinterende; *rad* radiärer Kanal; *rz* Randzacke; *sb.pl* Siebplatte; *sn.l* Sinneslinie; *tb* Tuberkel; *tb.so* Sockel des Tuberkels; *tb.tes* tuberkelartige Tessera; *tes* Tessera; *tes.so* Sockel der Tesserae; *v* Vorderende.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in der Höhe der Randzacken oder unmittelbar unter den Randzacken; dementsprechend sind die Ränder der Tesserae ebenfalls gezackt oder ausgeschnitten (Abb. 21 A und B). Aneinander grenzen die Tesserae mit einfachen Säumen. Dabei überlagern die vorderen Tesserae stets die hinteren in gleicher Weise wie freie Schuppen. Besonders ausgeprägt ist die schuppenartige Überlagerung an den kleinen und schmalen Tesserae des Seitenrandes des Panzers (Abb. 21 D, Abb. 25 F und G). Hier können sich sogar die vielfach zugespitzten Tesserae schräg nach hinten aufrichten, so daß sie äußerlich kleinen Hautzähnen eines Thelodontiers oder Selachiers ähneln. Seitenränder der Tesserae, die etwa parallel zur Mittellinie verlaufen, zeigen kein ausgeprägtes Überlagerungsverhältnis, wenn auch die medialen Tesserae häufiger die lateralen überlagern als umgekehrt. Oft findet auch keine Überlagerung an den Seitenrändern statt. In den Abbildungen 21 A und C sind die überlagerten Ränder durch unterbrochene Linien angedeutet, in den Abb. 25 F und G und Abb. 26 C und D durch dünne ausgezogene Linien. Unter dem binokularen Mikroskop kann man das Überlagerungsverhältnis meist unmittelbar wahrnehmen; auch läßt es sich mit einer feinen Nadel ertasten, wenn man die Nadelspitze gegen die Richtung der Tesserae-Ränder von hinten nach vorne gleiten läßt.

Längs den Sinneslinien (*sn.l*) klaffen die Ränder der Tesserae recht weit, es findet keine Überlagerung der Ränder statt (Abb. 21 A, Abb. 23 A). Die Sinneslinien heben sich bereits durch ihren geraden Verlauf heraus, die Grenzlinien zwischen den Tesserae bilden meist unregelmäßige Zickzacklinien. Die Sinneslinien können auch unmittelbar an die Tuberkel grenzen (Abb. 22 E). Alle Tesserae sind voneinander durch Spalten (*sp*) getrennt, die in die Circumarealkanäle (*cik*) des Porenkanalsystems führen. Eine Unterscheidung von Circumareal- und Intraarealkanälen nach der Höhenlage und nach dem Durchmesser der Kanäle ist nicht möglich; ihrer Anordnung und Ausbildung nach entsprechen sie den Circumarealkanälen. Sie sind breit und niedrig, die aus ihnen aufsteigenden Spalten, die die Porenkanäle vertreten, sind dagegen sehr schmal. Längs den Tuberkeln steigen sie schräg aufwärts (Abb. 22 E und F,

Abb. 22. *Dartmuthia gemmifera* Patten; A Bruchstück mit abgebrochenen Tesserasockeln und sichtbaren Siebplatten; × 25; f 698. B Bruchstück mit Beschädigung der Tesserae und Siebplatten, wodurch die Sockel der Tuberkel und der Boden der Circumarealkanäle sichtbar werden; f 699; × 25. C Bruchstück mit abgebrochenen Tesserae, wodurch die Siebplatten sichtbar werden; f 700; x 25. D Schliff Nr. 2529 Berlin; vertikaler Längsschliff durch Tuberkel; × 100. E Schliff Nr. 2517 Berlin; vertikaler Querschnitt durch Oberschicht mit Sinneslinie (links); × 100. F Schliff Nr. 2527 Berlin; vertikaler Querschliff durch Tuberkel und angrenzende Tessera; × 100. *cik* Circumarealkanäle; *dn* Mesodentin; *gfk* Gefäßkanal; *isp* Isopedin; *kz* Knochenzelle; *plk* Pulpakanal; *rad* radiäre Kanäle zwischen Tuberkeln und Tesserae; *rz.h* Randzacken am Hinterende; *rz.v* Randzacken am Vorderende des Tuberkels; *sb.pl* Siebplatte; *sn.l* Sinneslinie; *sp* Spalte der Circumarealkanäle; *tb* Tuberkel; *tb.so* Sockel des Tuberkels; *tb.tes* tuberkelartige Tesserae; *tes* Tessera; *tes.so* Sockel der Tesserae.

Abb. 23), zwischen den aufeinander folgenden Tesserae steigen sie zu Anfang senkrecht hoch, dann biegen sie sich horizontal seitwärts und münden schließlich nach oben, so daß der Querschnitt der Spalte zweifach geknickt erscheint (Abb. 23 B; 24 A und C). Dieser Knick ist durch das Überlagerungsverhältnis der Tesserae bedingt. Die vorderen Tesserae bilden den überlagernden (*üb.r*), die hinteren den unterlagernden Rand (*unt.r*).

Die Circumarealkanäle sind — ähnlich wie bei *Trematapis* — durch Siebplatten (*sb.pl*) in einen oberen und einen unteren Kanal unterteilt. Nur der untere Kanal wird von seitlichen oder aufsteigenden Gefäßkanälen versorgt, der obere nicht. Der obere Kanal ist viel höher als der untere (Abb. 24 A), meist auch breiter (Abb.23). Zwischen den unmittelbar aneinander grenzenden Randtuberkeln des Dorsalpanzers fehlen anscheinend Siebplatten (Abb. 26 H), die Kanäle zwischen den Tuberkeln münden senkrecht nach oben.

Die Siebplatten sind bei 50-facher Vergrößerung schon deutlich mit dem binokularen Miskroskop zu erkennen. Sie erscheinen als schneeweiße Schleier, die sich scharf von dem dunkelbraunen Knochen der Tuberkel und der Mittelschicht des Panzers abheben (Abb. 22 A—C). Selbst die Perforierung der Siebplatten deutet sich als allerfeinste Musterung an. Die Luft im schmalen Hohlraum unter den Siebplatten reflektiert das Licht, daher die schneeweiße Färbung in auffallendem Licht. Die Poren des Siebplatten (Abb. 25 D—E) sind kreisrund oder oval, meist etwas größer als bei *Trematapis* und daher leichter zu sehen. Ihr Durchmesser beträgt etwa 4—7 μ; ihre relative Größe bedingt auch ihren relativ geringeren Abstand im Vergleich zu *Trematapis*.

Die Tesserae haben, wie bereits Denison zeigte, die Gestalt einbeiniger Tische, die breite Tischplatte sitzt auf einem mittleren Sockel (*tes.so*), der einen dreieckigen oder ovalen Querschnitt hat (Abb. 22 A und C; Abb. 23; Abb. 24 C; Abb. 25 A—C, F und G; Abb. 26 C und D). Brechen die Platten ab, so bleiben die Sockelflächen oft stehen (Abb. 22 A und C). Zwischen den Sockeln der Tesserae und den Unterrändern der Tuberkel spannen sich die Siebplatten aus, die man bei ausreichender Vergrößerung in der Aufsicht sehen kann. Sie hängen meist ein wenig nach unten durch (Abb. 22 und 23), worauf schon die Anordnung der Siebporen hinweist (Abb. 25 C, rechts). Sie sind auch in den Sinneskanälen (*sn.l*) ausgespannt, hier aber meist ein wenig nach oben gewölbt (Abb. 22 E links, Abb. 23 A rechts). Durch die hart randlichen Siebporen erscheinen die Ränder der Siebplatten (*sbpl.a*), die an die Tuberkel oder die Sockel der Tesserae grenzen, fein gezackt (Abb. 25 A—C; Abb. 26 E und F). Die Siebplatten überspannen frei die radiär aus den Tuberkeln zu den Sockeln der Tesserae laufenden Kanäle (*rad*); vielfach aber verwachsen sie mit den Knochenleisten (*knl*) zwischen den Kanälen, wobei die Perforierung verschwindet (Abb. 22 A und C; Abb. 25 A—C). In der Aufsicht erscheinen diese Unterbrechungen der Perforierung durch die unterlagernden Knochenleisten als dunkle Striche (Abb. 22 A und C). Am Tuberkel setzen die Siebplatten unmittelbar über den austre-

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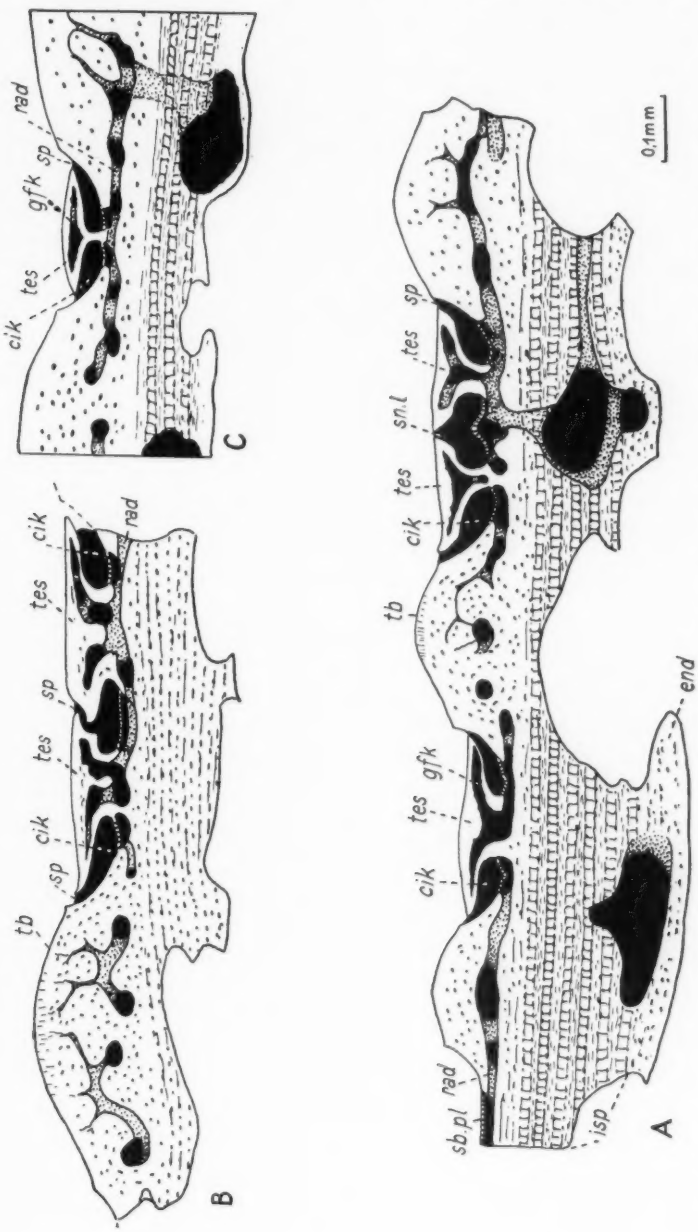
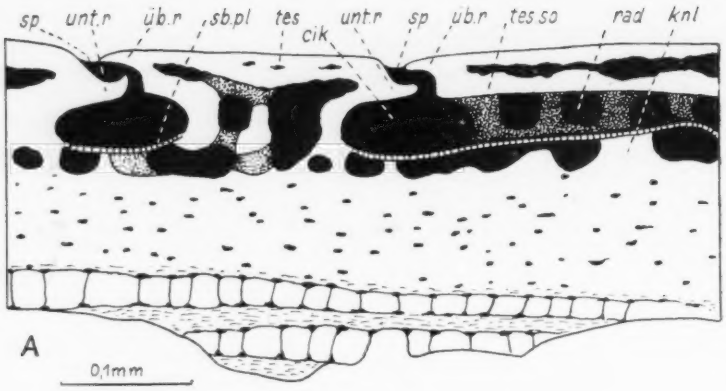


Abb. 23. *Dartmuthia gemmifera* Patten. Vertikalschliffe durch Tuberkel und Tesserae; × 100. A Schliff Nr. 2543 Berlin; zeigt rechts einen Sinneskanal zwischen Tesserae, ferner Isopedin mit anhaftendem Endoskelett. B Schliff Nr. 2518 Berlin; zeigt die Überlagerung benachbarter Tesserae. C Schliff Nr. 2542 Berlin; Tessera mit schmalem Ende des Sockels. *cik* Circumarealkanäle; *end* Endoskelett; *gfk* Gefäßplexus; *isp* Isopedin; *rad* radiärer Kanal zwischen Tuberkel und Tesserae; *sb.pl* Siebplatte; *sn.l* Sinneskanal; *sp* Spalte der Circumarealkanäle; *tb* Tuberkel; *tes* Tesserae.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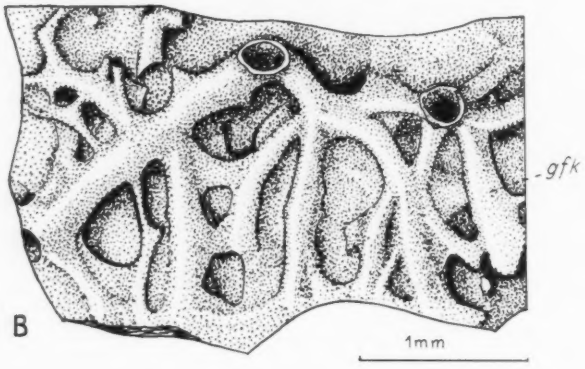
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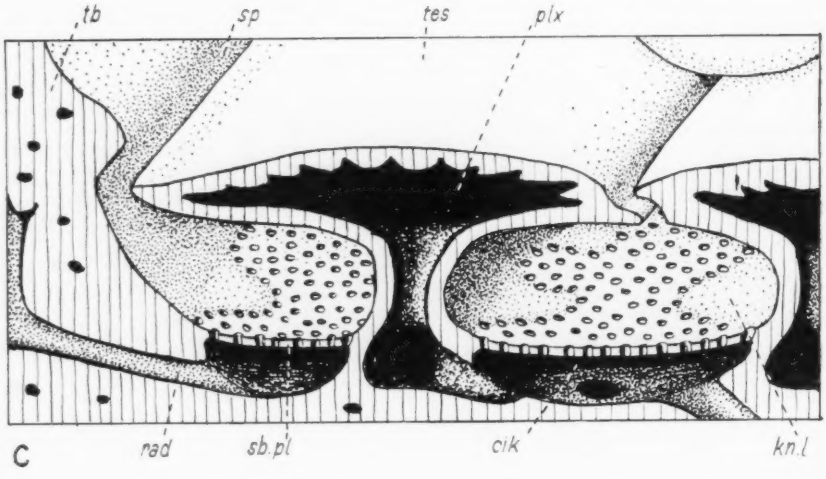
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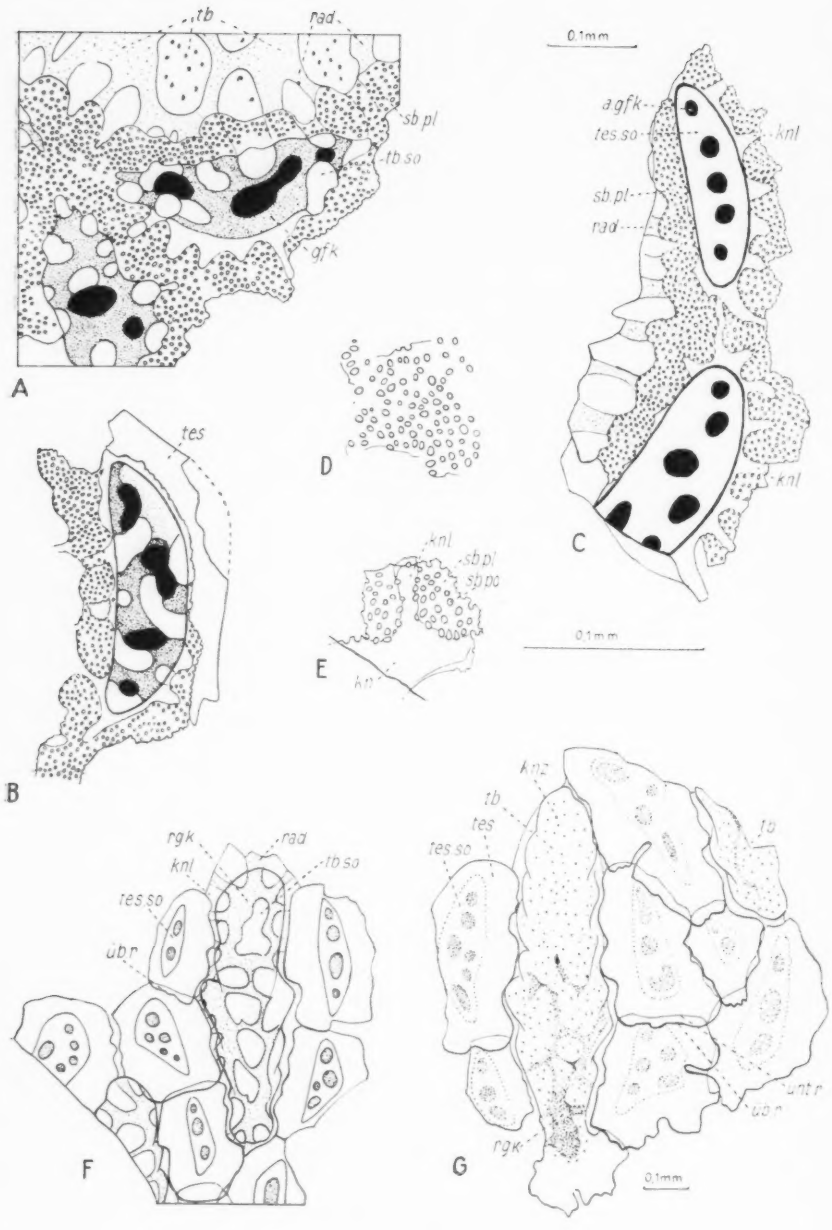
tenden radiären Kanälen (*rad*) an (Abb. 22 C und F; 26 E).

Nicht alle Tesserae sind eben. Recht häufig finden sich alle nur denkbaren Übergänge zu Tuberkeln (*tb.tes*). Ein meist etwas kleinerer und niedrigerer Tuberkel ist in solchen Fällen nicht allseitig von einer Spalte umgeben, sondern breitet sich in eine Tesseraplatte aus (Abb. 21 A, rechts über dem mittleren großen Tuberkel; Abb. 22 A). Es kann sich auch eine große Tesseraplatte in der Mitte buckelförmig aufwölben und längs einer ganz kurzen Erstreckung der Aufwölbung von einer Spalte begrenzt werden (Abb. 21 A, links). Andere Tesseraplatten zeigen nur in der Mitte eine niedrige Aufwölbung, ohne Einfluß auf die Begrenzung der Platte (Abb. 21 A, rechts neben dem mittleren großen Tuberkel). Das Auslaufen des Hinterendes eines langgestreckten Tuberkels in eine kleine Tesseraplatte sehen wir auf Abb. 21 D und Abb. 25 G. Je nach dem Grad der Aufwölbung ist die Braunfärbung stärker oder schwächer. Die ganz niedrigen Aufwölbungen sind hellgelblich oder bräunlich; sie zeigen unter dem Mikroskop bereits einige Knochenzellen. Höhere Aufwölbungen werden braun bis dunkelbraun und sind erfüllt von zahlreichen Knochenzellen und Pulpakanälen, die in den Tesseraplatten sonst fehlen. Es besteht demnach kein grundsätzlicher Unterschied zwischen Tuberkeln und Tesserae, beide Gebilde können in beliebigem Grade ineinander übergehen; die Tesserae sind differenzierte Tuberkelsockel.

Der Dorsalpanzer von *Dartmuthia* setzt sich aus drei Schichten zusammen: aus der Oberschicht mit Tuberkeln, Tesserae und eingeschlossenem Porenkanalsystem; aus einer dünnen Mittelschicht mit Gefäßkanälen verschiedenen Durchmessers und aus der Unterschicht, die aus typischem Cephalaspiden-Isopedin besteht. So ist der Panzer im hinteren Abschnitt, der nicht von Endoskelett unterlagert wird, aufgebaut. Im Bereich des Endocraniums schließt sich unmittelbar an das Isopedin das Knochengewebe des Endoskelettes in Gestalt zahlreicher Knochenröhren für Blutgefäße und Nerven. Oft kleidet eine ganz dünne Schicht des Endoskelettes die Unterseite des Isopedins aus und geht kontinuierlich in die Wände der Gefäßkanäle über. Die überaus zahlreichen knochenumwandeten Kanäle bieten einen ganz ungewohnten Anblick, wie wir ihn von Knochen rezenter Wirbeltiere nicht kennen (Abb. 24 B).

Abb. 24. *Dartmuthia gemmifera* Patten. A Schliff Nr. 2531 Berlin; zeigt die Überlagerung der Tesserae und rechts den Tesserasockel mit angrenzender Siebplatte; × 200. B Bruchstück der Vorderhälfte des Panzers von unten, mit anhaftendem Endoskelett, das das Isopedin bekleidet und Gefäße umwandet; f 701; × 25. C schematische Darstellung eines angeschnittenen Tuberkels und zweier Tesserae mit Siebplatten; etwa × 400. *cik* Circumarealkanal; *gfk* Gefäßkanal im Endoskelett; *kn.l* Knochenleiste zwischen radiären Kanälen, Siebplatte stützend und z.T. mit ihr verwachsen; *plx* Gefäßplexus in der Tesseratafel; *rad* radiäre Kanäle zwischen Tuberkel und Tesserae; *sb.pl* Siebplatte; *sp* Spalte der Circumarealkanäle; *tb* Tuberkel; *tes* Tesserae; *tes.so* Sockel der Tesserae; *üb.r* überlagernder Rand der Tesserae; *unt.r* unterlagernder Rand der Tesserae.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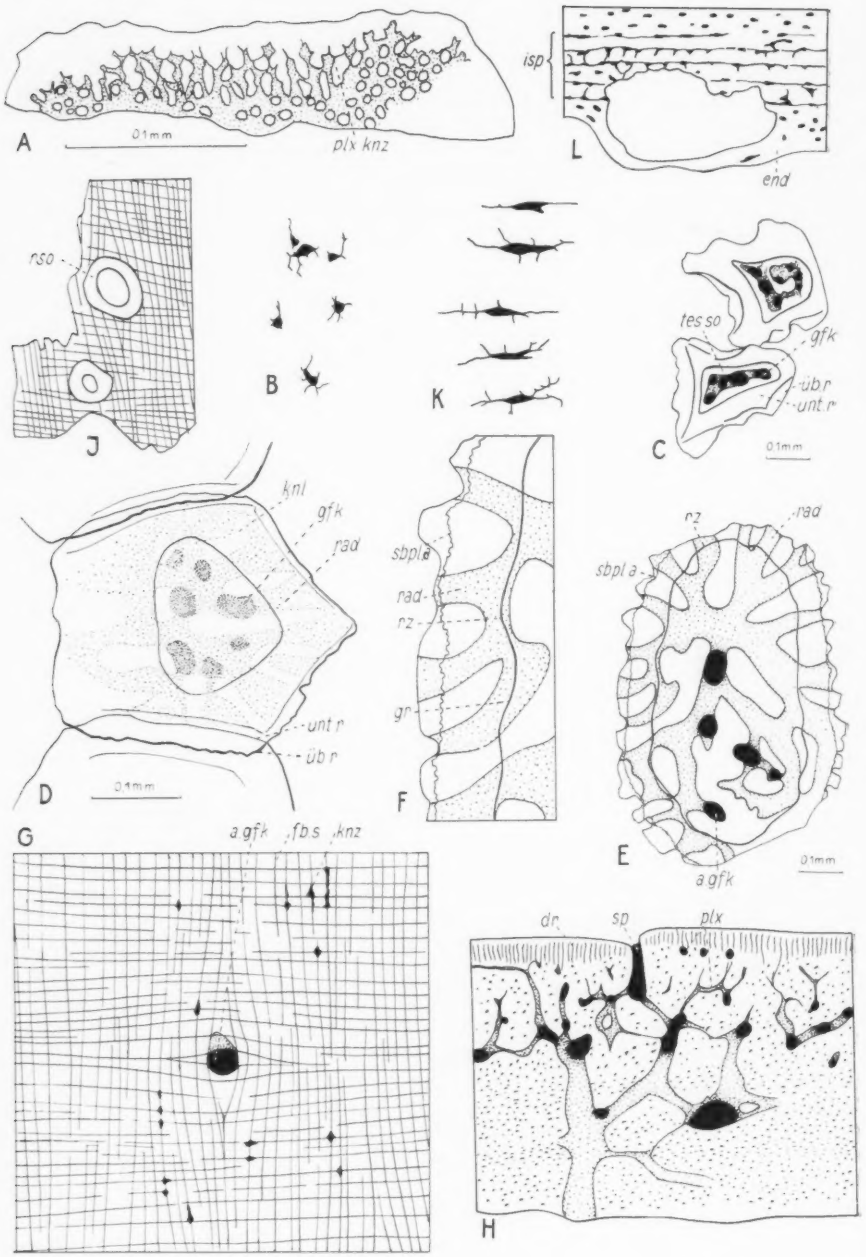
Die Unterschicht ist typisches Isopedin, aufgebaut aus sich regelmäßig überkreuzenden Faserbündeln zwischen denen sich zellenartige Lakunen (*knz*) finden (vgl. Gross 1956 S. 111—112), deren Gestalt oft ganz unregelmäßig wird. Die von unten aufsteigenden Gefäßkanäle drängen die Gefäßbündel etwas auseinander, aber umwanden sich nicht mit einem primären Osteon (Abb. 26 G), obgleich sich die Kanäle nach unten im Endoskelett fortsetzen können. In den großen durch Resorption oder zu geringe Verknöcherung entstandenen Höhlen des Isopedins sind die Einmündungen der aufsteigenden Kanäle oft von einem niedrigen Knochensockel (Abb. 26 J) umgeben, den die Resorption (?) anscheinend übrig ließ. Schaut man mit dem binokularen Mikroskop in die Höhlen des Isopedins, so kann man vielfach die schwellenförmigen Sockel am Boden der Höhlen sehen.

Im Gegensatz zum Isopedin besteht das Endoskelett aus echtem Knochen mit vielfach sehr ausgeprägten, langen spindelförmigen Knochenzellen (Abb. 26K), wie sie sich im Exoskelett von *Trematapis* oder *Dartmuthia* sonst nicht finden. Sie gleichen weitgehend den spindelförmigen Knochenzellen in der Unterschicht der Antiarchi und Rhipidistia. Das Isopedin der Cephalaspida ist recht hell und durchsichtig im Gegensatz zum typischen Knochengewebe der Mittelschicht und der Tuberkel. Mit dem Knochengewebe dieser höheren Schichten stimmt das Knochengewebe des Endoskelettes im Besitz typischer Knochenzellen und der braunen Farbe überein. Das Isopedin der Cephalaspida ist kein echtes Knochengewebe, sondern verknöchertes, sehr regelmäßig gebündeltes Bindegewebe. Im Isopedin finden sich vielfach große Hohlräume ohne eigene Lamellenumwandung; ihre Verbreitung ist unabhängig von der der Tuberkel. Eigenartig sind die Höhlen an der Grenze zwischen Isopedin und Endoskelett: die ins Isopedin ragende Hälfte sieht wie ein Resorptionsraum aus, die Unterhälfte wird dagegen von den Lamellen des endoskelettalen Knochens wie von einem primären Osteon umgeben (Abb. 26 L).

Aus der Unterschicht treten die Gefäße in die Mittelschicht, wo sie sich sogleich mit primären Osteonen umwanden können; in der Mittelschicht findet sich meist nur eine Lage von horizontalen Kanälen. Unter den Tuberkeln bilden sie

Abb. 25. *Dartmuthia gemmifera* Patten. Horizontalschliffe. A Schliff Nr. 2535 Berlin; Siebplatten zwischen Tuberkeln und Tesserae; × 125. B Schliff Nr. 2535 Berlin; Tesserasockel und Siebplatten; × 125. C Schliff Nr. 2535 Berlin; Tesserasockel mit Siebplatten, radiären Knochenleisten und aufsteigenden Gefäßkanälen; × 125. D Schliff Nr. 2537 Berlin; Siebplatte; × 255. E Schliff Nr. 2536 Berlin; Siebplatte und radiäre Knochenleiste; × 255. F Schliff Nr. 2539 Berlin; Tuberkel zwischen sich überlagernden Tesserae, zeigt die ringförmigen und radiären Gefäßkanäle in der Basis; × 65. G Schliff Nr. 2538 Berlin; zeigt Tuberkel, der am Hinterende in Tessera übergeht, und die Überlagerung der Tesserae; × 65. *a.gfk* aufsteigender Gefäßkanal; *gfk* Gefäßkanal; *kn* Knochen; *knl* Knochenleiste zwischen radiären Kanälen; *knz* Knochenzellen; *rad* radiäre Kanäle; *rgk* ringförmige Gefäßkanäle in der Tuberkelbasis; *sb.pl* Siebplatte; *sb.po* Poren der Siebplatte; *tb* Tuberkel; *tb.so* Sockel der Tuberkel; *tes* Tesserae; *tes.so* Sockel der Tesserae; *üb.r* überlagernder Rand der Tesserae; *unt.r* unterlagernder Rand.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oft unregelmäßig ring- oder halbringförmige Schlingen (Abb. 25 F und G, *rgk*), aus denen steil oder schräg nach oben enge subepidermale (*plk*) Kanäle aufsteigen. Ihre Wände sind von den beherbergten Zellen ausgezackt (Abb. 22 E und F). Oben bilden sie mit arkadenförmigen Verbindungen einen besonderen Plexus, aus dem die Ausläufer der Zellen strahlen. Die Ausläufer nehmen wie immer in den Spitzen der Tuberkel eine besonders regelmäßige, parallele und senkrechte Anordnung in der Art der Dentinröhrchen an, so daß dieser Teil des Tuberkels aus Mesodentin aufgebaut wird. Leider lassen sich an meinen Schliffen diese dentinröhrchenartigen Ausläufer nicht deutlich verfolgen (Abb. 22 F).

Aus den Gefäßschlingen (*rgk*) an der Basis des Tuberkels zweigen sehr regelmäßig nach allen Seiten in radialer Anordnung enge Kanäle (*rad*) ab, die man schon in der Aufsicht durch ihre hellen Kalkausfüllungen durch den Knochen schimmern sieht (Abb. 21 G; Abb. 22 A, B und C). In Horizontalschliffen durch die Tuberkel treten sie deutlich hervor (Abb. 26 E und F; Abb. 25 F). Sie münden an der Basis des Tuberkelsockels nach außen und streben zu den Sockeln der Tesserae. Zwischen Tuberkel und Tesserasockel verlaufen sie nicht als geschlossene Kanäle, sondern als offene Rinnen, die durch Knochenleisten getrennt werden (Abb. 21 G; Abb. 22 A—C). Jeder Tuberkel ist von einem Kranz radial ausstrahlender Rinnen oder Furchen in der Oberfläche der Mittelschicht umgeben. Diese Furchen werden von den Siebplatten überwölbt, die — wie bereits gesagt — gelegentlich mit den Knochenleisten (*knl*) verwachsen (Abb. 24 A; Abb. 25 A—C und E). Die radiär angeordneten Kanäle (*rad*) entsprechen ähnlichen Kanälen von *Trematapsis* (Gross 1956, Abb. 86 A und C), die aber von unten in die Maschenkanäle münden. Bei *Dartmuthia* bilden sie

Abb. 26. *Dartmuthia gemmifera* Patten. Dünnschliffe. A Schliff Nr. 2523 Berlin; Rand der Tessera mit plexusartigem Hohlraum, von oben; × 255. B Schliff Nr. 2539; Knochenzellen im Tuberkel; × 255. C Schliff Nr. 2538 Berlin; Horizontalschliff durch Tesserasockel, von unten; × 65. D Schliff Nr. 2536 Berlin; Tessera mit radiären und aufsteigenden Gefäßen, von oben; × 125. E Schliff Nr. 2541 Berlin; Horizontalschliff durch Tuberkel mit Ringgefäß, radiären Gefäßen, aufsteigenden Gefäßen, Ansatz der Siebplatte und Randzackensaum; × 65. F Schliff Nr. 2541 Berlin; vergrößerter Ausschnitt aus Fig. E zur Verdeutlichung des Ansatzes der Siebplatte; × 125. G Schliff Nr. 2523 Berlin; Horizontalschliff durch das Isopedin (Unterschicht) mit aufsteigendem Gefäßkanal; × 65. H Schliff Nr. 2534 Berlin; vertikaler Längsschliff durch Randtuberkel; × 65. J Schliff Nr. 2535 Berlin; Aufsicht auf das Isopedin am Boden der großen Höhlen der Unterschicht mit Knochensockel um die aufsteigenden Gefäßkanäle; × 65. K Schliff Nr. 2521 Berlin; spindelförmige Knochenzellen des Endoskelettes; × 255. L Schliff Nr. 2542 Berlin; Vertikalschliff durch das Isopedin und anhaftendes Endoskelett, einen Hohlraum der Unterschicht umfassend; × 125; (vgl. Abb. 23 C). *a.gfk* aufsteigende Gefäßkanäle; *dr* Dentinröhrchen; *end* endoskelettaler Knochen; *fb.s* Faserbündelscheiden; *gfk* Gefäßkanal; *isp* Isopedin; *knl* Knochenleiste zwischen radiären Kanälen; *knz* Lakunen der Knochenzellen; *plx* Gefäßplexus unter den Dentinröhrchen; *plx.knz* Plexus in der Tesseraplatten mit lakunenartigen Randbildungen; *rad* radiäre Kanäle; *rso* ringförmiger Knochensockel um aufsteigende Gefäßkanäle des Isopedins; *rz* Randzacken der Tuberkel; *sbpl.a* Siebplattenansatz; *sp* Spalten der Circumarealkanäle; *tes.so* Sockel der Tesserae; *üb.r* überlagernder Rand der Tesserae; *unt.r* unterlagernder Rand.

dagegen offene Furchen in der Unterhälfte der Circumarealkanäle, die keine gesonderte untere Wand oder einen gegen die versorgenden Blutgefäße abgesetzten Boden haben. Die Unterhälfte der Circumarealkanäle wird auch gelegentlich unmittelbar von senkrecht aus der spongiösen Mittelschicht aufsteigenden Gefäßkanälen versorgt (Abb. 22 E; Abb. 23 A). Die radiären Kanäle liegen auf der Oberfläche der Mittelschicht, sie sind daher nicht mit den echten Radialkanälen (radiating canals) der Mittelschicht vieler polygonaler Platten großer Cephalaspiden zu vergleichen, die zudem in mehreren Schichten übereinander liegen. Die Frage nach dem Zusammenhang der großen Tesserae oder Plättchen der Cephalaspidae mit den von Maschenkanälen oder Circumarealkanälen umgebenen kleinen Tesserae oder Polygonen von *Trematapis* und *Dartmuthia* muß noch geklärt werden.

Die Tesseraesockel sind meist schmale, im horizontalen Querschnitt oft ovale Gebilde (Abb. 25). In Vertikalschliffen erscheinen sie entweder als schmale Stiele eines „Pilzes" (Abb. 23 A und C) oder als breite Stützen (Abb. 24 A), je nachdem ob sie der Länge oder Quere nach getroffen sind. Die von den Tuberkeln kommenden radiären Kanäle bzw. Furchen treten ebenfalls radiär in die Basis des Sockels ein, in der sie sich zu unregelmäßigen Schlingen vereinigen (Abb. 25 A—C; Abb. 26 C). Aus der Schlinge erheben sich mehrere senkrecht aufsteigende Kanäle (Abb. 23, 24 A, 25 und 26 C), vergleichbar den aufsteigenden Kanälen (*plk*) in den Tuberkeln. In der Tesseraplatte breiten sich diese Kanäle aus und verbinden sich untereinander zu einem niedrigen und breiten Hohlraum oder Plexus (*plx*), der sich an den Rändern in unregelmäßige lakunenartige Zacken und Fortsätze auflöst (Abb. 26 A, *plx.knz*). Es kommt nur selten zur Bildung von klar begrenzten, getrennten und mit Ausläufern versehenen Knochenzellen. Der äußerste Rand der Platte ist frei von Hohlräumen und glasklar. Sobald sich aber die Platten nur ein wenig wölben, treten normale Knochenzellen auf, die denen der Tuberkel völlig gleichen. Die Ausbildung von Knochenzellen ist einfach an die Ausdehnung bzw. die Dicke der Tesseraplatte gebunden, dünne Platten bieten keinen ausreichenden Raum.

Die eigentümliche Gestalt der Tesserae von *Dartmuthia* wird anscheinend durch die relativ große Breite der Maschenkanäle bedingt, die die Unterhälfte der Tesserae zu einem schmalen Sockel einschnüren. Der Durchmesser der Maschen des Porenkanalsystems stimmt im Durchschnitt etwa mit der Maschenweite bei *Trematapis mammillata* überein (375 μ); *Trematapis schmidti* hat meist engere Netzmaschen (150—200 μ). Die Breite der Tesseraplatten von *Dartmuthia* kann auch 600—700 μ erreichen. Die Längs der Tuberkel schwankt zwischen 2000 und 500 μ, oft beträgt sie 750 μ; die Maschenkanäle sind 80 bis 100 μ breit, bei *Trematapis* nur 30—50 μ.

Die Übergangsformen zwischen Tuberkeln und Tesserae zeigen, daß hier keine grundsätzlichen Unterschiede vorliegen, Tuberkel und Tesserae ent-

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sprechen beide den polygonalen, durch die Circumarealkanäle bedingten Bezirken im Ventralpanzer. Die Tuberkel haben die Höhe und die Ausbildung der Polygone behalten, die Form (Umriß) aber geändert, die Tesserae haben den Umriß behalten, sind aber kleiner und niedriger geworden, eine Platte mit stielförmigem Sockel, die keine Deckschicht aus Mesodentin trägt. Eine weiterschreitende Reduktion der Höhe der Tesserae würde zu ihrem Verschwinden führen, es blieben nur noch die isolierten Tuberkel nach, wie wir sie bei manchen Cephalaspida finden. Tuberkel und Tesserae gehören bei *Dartmuthia* einer einzigen Generation an, sie sind Differenzierungen einer ehemals geschlossenen, knöchernen, oben mesodentinartigen Oberschicht, wie wir sie bei *Trematapis* finden.

Trematapis und *Dartmuthia* zeichnen sich durch das gleiche Merkmal des Besitzes von Siebplatten aus. Es ist zu hoffen, daß auch die anderen gleichalten Osteostracen-Gattungen aus Oesel daraufhin untersucht werden, ob sie Siebplatten oder ähnliche Bildungen in ihrem Porenkanalsystem aufweisen. Mir steht leider kein Material zur Verfügung.

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Zusammenfassung der Ergebnisse

1) Nur eine einzige Heterostracen-Gattung findet sich verbreitet, wenn auch immer spärlich im Beyrichienkalk, die Gattung *Oniscolepis* Pander. Unter diesem Namen werden die beiden Panderschen Gattungen *Oniscolepis* und *Strosipherus* vereinigt. In den rotbunten, etwas sandigen Kalken über dem Beyrichienkalk fehlt diese Gattung.

2) In den dolomitischen Beyrichienkalken, die durch das Fehlen von *Thelodus parvidens* und die Häufigkeit von *Thelodus* (*Turinia* ?) cf. *scoticus* gekennzeichnet sind, erscheinen erstmalig mit spärlichen Resten die Heterostracen-Gattung *Traquairaspis* und die Osteostracen-Gattung *Zenaspis* ?, die beide in den rotbunten Kalken (Bey. 36 und 37) häufig sind. Zu ihnen treten in den rotbunten Kalken die Gattungen *Anglaspis* und *Corvaspis*, ferner eine weitere, noch unbestimmte Osteostracen-Gattung. In einem anderen, kalkigen Geschiebe (Bey. 38) finden sich neben zahlreichen besonders gut erhaltenen Resten von *Zenaspis* ? sp. indet. Schuppen einer Anaspiden-Gattung (Gross 1958), es fehlen aber hier die eben genannten Heterostraci gänzlich. *Traquairaspis* ist von Brotzen (1934) und von Gross (1947) unter dem Namen *Orthaspis* Brotzen beschrieben worden. Die Gesteine mit diesen Heterostracen- und Osteostracen-Resten haben ein jüngeres Alter als die Invertebraten-führenden Beyrichienkalke.

3) *Traquairaspis* Kiaer sp. indet. ist an den großen, weitgetrennten und gezackten Skulpturen leicht zu erkennen; auf dem Panzer dieser Gattung bilden sich keine typischen Zwischenfurchen, da der Abstand der Skulpturen zu weit ist. Sehr charakteristisch ist auch die geschlossene glatte Dentindecke des zen-

tralen Feldes des Ventralschildes. Die Sinneslinien münden zwischen den Skulpturen. An bestimmten Stellen des Panzers oder vielleicht auf den Schuppen kommt es zu wiederholter Dentinbildung in sehr regelmäßiger Weise. Die Skulpturen der ersten Dentingeneration werden in gleicher Anordnung von größeren Skulpturen einer zweiten und vermutlich auch dritten Generation überlagert. Der Bildung der neuen Dentingeneration geht eine Resorption der Oberhälfte der Dentinleisten voraus, wodurch die älteren Dentinleisten eine fast ebene Oberfläche erhalten, auf der die eröffneten Dentinröhrchen und Pulpakanäle münden. Einzelne größere Dentinleisten umschließen manchmal kleinere ältere Dentinleisten, die vor der Bedeckung durch die sekundären Leisten keine Resorption erfahren haben.

4) *Anglaspis* Kiaer sp. indet. ist an der Skulptur und deren Anordnung auf den Schuppen leicht zu erkennen. Alle Leisten haben einen scharfen Grat; auf den Schuppen sind sie in geraden Längsreihen angeordnet, vor denen einige gerade Querleisten liegen. Die Leisten grenzen nicht selten so eng aneinander, daß sich die Rinnen zwischen ihnen schließen oder nur mit Reihen enger Poren münden. Charakteristisch ist die Art der Verästelung der Dentinröhrchen. Meist bedecken die Dentinleisten unmittelbar die rechteckigen Spongiosakammern, die damit zu Pulpahöhlen bzw. Pulpakanälen werden. Die engen hochgelenen Verbindungskanäle der unter einer Leiste liegenden Kammern strahlen ebenso Dentinröhrchen aus wie die Oberhälfte der Spongiosakammern. Keine Dentinröhrchen werden dagegen von den tieferliegenden Verbindungskanälen der Spongiosakammern zu den Zwischenrinnen und den Spongiosakammern der Nachbarleisten ausgestrahlt. Sehr schön lassen sich Bildungsstadien des Dentins und des Aspidins beobachten; beide Gewebearten können kontinuierlich ineinander übergehen.

5) *Corvaspis* Woodward sp. indet. ist bisher nur durch die charakteristischen, vorne dick angeschwollenen Schuppen vertreten, deren Skulpturen meist im Zentrum der Schuppe am längsten und breitesten sind. Die Zwischenrinnen sind unten absatzartig eingeschnürt, doch nicht von einer Knochenmembran in eine obere und untere Abteilung getrennt. Die Verbindungskanäle zwischen den Pulpakanälen und den Zwischenrinnen münden fast senkrecht von unten in die Zwischenrinnen. Das Dentin der Leisten ist sehr regelmäßig geschichtet und geht vielfach kontinuierlich in das angrenzende Aspidin über.

6) *Oniscolepis* Pander sp. indet. Unter diesem Namen werden alle Reste vereinigt, die Pander (1856) als *Oniscolepis* und *Strosipherus* und Gross (1947) als *Strosipherus* beschrieben haben. Die Reste sind Schuppen oder dicke Tesserae von polygonaler Gestalt. Die Dentinleisten sind meist angedeutet konzentrisch angeordnet, in der Mitte die kleinsten und zierlichsten Dentinleisten, außen die größten und breitesten. Zu Beginn der Dentinbildung gehen die Dentinröhrchen von großen Längskanälen unter den Leisten aus, in späteren Stadien von einzelnen aufsteigenden Pulpakanälen. Die Querkanäle zwischen den Pulpa-

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kanälen und den Zwischenrinnen sind auffallend regelmäßig angeordnet und bilden meist auch die Verbindung zu den Pulpakanälen der Nachbarleisten. Die Zwischenrinnen zeichnen sich durch eine besonders ausgeprägte Absatzbildung aus. Die Tesserae sind dicker als die Schuppen, ihre Ränder fallen steil ab und haben keine Überlagerungsflächen.

7) *Tolypelepis* Pander. Vermutlich ist *Tolypelepis* im Beyrichienkalk durch einige wenige, nicht sicher bestimmbare Reste vertreten. Der Aufbau des Panzers dieser Gattung erinnert etwas an *Anglaspis;* es finden sich verschiedene Bildungsstadien, der Aufbau ist nicht so einheitlich, wie ihn Bystrow (1955) beschreibt. Die Verbindung der Spongioskammern bzw. Pulpahöhlen unter den Dentinleisten ist die gleiche wie bei *Anglaspis.*

8) Bei allen beschriebenen Heterostraci lassen sich die verschiedensten Bildungsstadien des Dentins und des Aspidins finden; man muß die Merkmale der Bildungsstadien von den gattungsspezifischen Merkmalen streng unterscheiden. Die Dentinbildung geht allem Anschein nach stets von Gefäßkanälen (Pulpakanälen) aus, die zu Beginn der Dentinbildung inmitten kolloidalen, unverkalkten Dentins in weiten Hohlräumen (Pulpahöhlen) bereits ihre spätere Stellung einnahmen. Weite, unter den Dentinleisten verlaufende Höhlen oder Kanäle werden später durch Zwischenwände unterteilt und verengen sich wiederum in Fortsetzung der Dentin- und Aspidinbildung zu aufrechten Pulpakanälen. Diese Einengung des Hohlraumes brauchte keineswegs immer einzutreten. Vielfach bildeten sich Dentin und das angrenzende Aspidin gleichzeitig, ihre Feinlamellen gehen ohne Unterbrechung ineinander über, der Unterschied liegt nur im Vorhandensein oder Fehlen von Dentinröhrchen. — Die Gefäße im Dentin und im Aspidin umwanden sich mit feinen Lamellen, es entstehen Skelettröhren völlig homolog zu den primären Osteonen des Knochens; für diese Gefäßumwandungen werden die Bezeichnungen „Dentone" und „Aspidone" eingeführt. Sie heben sich gegen das oft reichlich mit Sharpeyschen Fasern erfüllte primäre Hartgewebe deutlich ab. Die große Rolle der Gefäße bei der Dentinbildung weist vielleicht darauf hin, daß den Dentinskulpturen der Heterostraci echte Pulpagebilde, wie sie sich den Pulpahöhlen der Mundzähne der Gnathostomen finden, gefehlt haben.

Noch kann die Frage nicht entschieden werden, ob die Heterostraci auch ein Porenkanalsystem besessen haben oder nicht. Die Anordnung der Zwischenrinnen, ihr Querschnitt und ihre Versorgung durch aufsteigende Gefäßkanäle und ihre Querverbindungen mit den Pulpakanälen erinnern auffallend an die Maschen- und Porenkanäle der Osteostraci, Rhipidistier und Dipteriden. Echte Porenkanäle sind bei Heterostraci nie gefunden worden, auch wenn die Zwischenrinnen durch teilweisen Verschluß nur noch durch Porenreihen münden können. Rücken die Dentinleisten weit auseinander, so fehlen Spuren etwaiger Maschen- und Porenkanäle genau wie bei manchen Osteostraci. Erst die Entdeckung von gesonderten Porenkanälen oder Siebplatten wären Beweise für das Vorhandensein eines Porenkanalsystems in den Zwischenrinnen.

9) *Zenaspis* Lankester ? sp. indet. Die von Gross (1956) als Knochenplättchen incertae sedis beschriebenen Reste sind Bruchstücke des Panzers oder der Schuppen eines Osteostracen, dessen Skulpturen am meisten an *Zenaspis excellens* (Wängsjö) erinnern. Sie werden daher unter der Bezeichnung *Zenaspis* ? sp. indet. beschrieben. Die meisten Reste sind von Skulpturen zweier Mesodentingenerationen bedeckt. Die primären Leisten sind recht weit getrennt und hochgewölbt. Zwischen ihnen entstehen neue Dentinleisten einer zweiten Generation, die sich mit Quersprossen (Querästen) an die primären Leisten stützen. Das Mesodentin der zweiten Generation hat etwas anders gestaltete und gerichtete Dentinröhrchen, nie gehen beide Dentingenerationen ineinander über. Das sekundäre Mesodentin kann sich auch als dünne oder als ganz dicke Schicht über die Leisten des primären Dentins legen, so daß diese äußerlich völlig verschwinden. Durch die Bildung der zweiten Mesodentingeneration wird das Porenkanalsystem, das bereits vorher zwischen den primären Dentinleisten ausgebreitet war, sichtbar. Zuerst erscheinen im Bildungsvorgang die Mündungen der Porenkanäle, dann diese selber und zuletzt die Maschenkanäle. Die großen Maschenkanäle entsprechen den Circumarealkanälen der Osteostraci, die kleinen, nicht selbständig von Blutgefäßen versorgten oberen Maschenkanäle sind Intraarealkanäle. Siebplatten sind in diesen verschiedenen Kanälen nicht vorhanden. Das sekundäre Mesodentin bildet sich wie alles Dentin von oben nach unten, von außen nach innen.

Zenaspis ? sp. indet. und *Porolepis* ähneln einander in der Bildung zweier Dentingenerationen, von denen die ontogenetisch zuerst gebildete aus isolierten Dentintuberkeln (Hautzähnen) oder Dentinleisten besteht, die ontogenetisch jüngere aus einer geschlossenen Dentindecke, die das Porenkanalsystem einschließt. Ontogenetisch ist die Generation der Dentinskulpturen die primäre, die Generation der geschlossenen Dentindecke die sekundäre. Gilt das auch für eine phylogenetische Betrachtung? Manche der ältesten bekannten Osteostraci (*Trematapis*) hatten eine geschlossenen Mesodentindecke; eine geschlossenen Dentindecke finden wir auch bei den Osteolepiden und Dipteriden. Viele jüngere Osteostraci und die Holoptychiiden (*Laccognathus* und *Glyptolepis* z. B.) haben nur gesonderte Dentinskulpturen, die geschlossenen Dentindecken sind verschwunden. Vermutlich ist die geschlossene Dentindecke das phyletisch primäre, die isolierten Dentinskulpturen das phyletisch sekundäre Gebilde. Die Verdrängung der geschlossenen Dentindecke ging vermutlich so vonstatten, daß in der Ontogenese — etwa bei *Zenaspis* ? sp. indet. und bei *Porolepis* — vor der Bildung der geschlossenen Dentindecke die isolierten Dentinskulpturen entstanden, die nachfolgend von der Dentindecke überdeckt und verhüllt wurden. Die Dentinskulpturen entstanden gewissermaßen proterogenetisch. Im weiteren Verlauf der Phylogenese wurde die geschlossene Dentindecke ontogenetisch unterdrückt, die Dentinskulpturen gerieten damit endgültig auf die Oberfläche des Exoskelettes (viele Osteostraci, *Laccognathus, Glyptolepis*). Sie repräsentieren nicht ein Ahnenstadium,

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das vor der phyletischen Bildung der geschlossenen Dentindecke existiert hatte. Bei den Osteolepiden schaltete sich in der Ontogenese kein Stadium der Bildung isolierter Dentinskulpturen ein, beim Verlust der geschlossenen Dentindecke wurde die Oberfläche des Exoskelettes sofort knöchern. Aber auch bei Formen, bei denen nun die Dentinskulpturen zur Herrschaft gelangt waren, wurden diese später durch Knochenskulpturen ersetzt (*Holoptychius*), die Dentinskulpturen verschwanden völlig.

10) Osteostraci: genus indeterminabile. Reste einer Osteostracen-Gattung können nicht sicher bestimmt werden. Die kräftigen Reste unterscheiden sich von *Zenaspis* ? sp. indet. durch den Bau der beträchtlich größeren und breiteren Skulpturen, die zur Hälfte oder gar zu zwei Dritteln aus Knochen bestehen, der oben ohne Absatzbildung von Mesodentin gekrönt wird. Aus dem breiten Knochensockel münden seitlich vielfach Blutgefäßkanäle in die Zwischenfurchen. Das Mesodentin ist der Größe der Skulpturen entsprechend ausgeprägt. Raumnetzartige Verbindungen der Dentinröhrchen, die sich vielfach zu Lakunen erweitern, sind sehr deutlich.

11) *Dartmuthia gemmifera* Patten. Zum Vergleich mit *Zenaspis* ? sp. indet. und mit *Trematapis* (Gross 1956) wurde *Dartmuthia* in die Untersuchung einbezogen, und zwar aus Materialgründen nur der Dorsalpanzer der Gattung. Der Ventralpanzer von *Dartmuthia* hat bekanntlich eine geschlossene Dentindecke wie *Trematapis*, jedoch münden die Circumarealkanäle nicht durch Porenkanäle, sondern durch Spalten von zickzackartigen Verlauf. Die oberste Knochenschicht des Ventralpanzers ist mesodentinartig. Die Oberfläche des Dorsalpanzers setzt sich dagegen aus hohen, ovalen Tuberkeln und niedrigen polygonalen Tesserae zusammen. Zwischen allen diesen Gebilden öffnen sich die breiten Circumarealkanäle mit bald einfachen (zwischen den Tesserae), bald mit etwas gezackten Spalten (zwischen Tuberkeln und Tesserae). Die Spalten zwischen den Tesserae münden meist nicht gerade nach oben, sondern in geknicktem Verlauf, da die vorderen Tesserae stets die nachfolgenden ein wenig überlagern, nach Art freier Körperschuppen. Unregelmäßig oder garnicht ausgeprägt ist ein derartiges Überlagerungsverhältnis zwischen seitlich nebeneinander liegenden Tesserae.

Die Sinneskanäle öffnen sich mit weit offenen Spalten in ziemlich geraden Linien. Sie sind genau so wie die Circumarealkanäle durch tiefliegende Siebplatten besonders schöner Ausprägung unterteilt in eine niedrige und meist schmale Unterhälfte und eine hohe und breite Oberhälfte; sie sind Bestandteile des Porenkanalsystems. Die Siebplatten überdachen offene radiale Furchen, Verbindungen zwischen den radiär verlaufenden Kanälen der Tuberkel und der Sockel der Tesserae. Diese radiären Furchen entsprechen den radiären Kanälen, die bei *Trematapis* von unten in die Circumarealkanäle münden und die Verbindung zwischen dem subepidermalen Gefäßplexus und den Circumarealkanälen herstellen. Die Verbindungskanäle sind bei *Dartmuthia* zwischen Tuberkeln und Tesserasockeln oder zwischen letzteren als offene Rinnen entwickelt.

Zwischen Tuberkeln und Tesserae besteht kein grundsätzlicher Unterschied, es lassen sich alle Übergangsformen finden. Durch den sockelartigen schmalen Fuß der Tesserae steigen die Gefäßkanäle hoch und breiten sich in der Tesseraplatte plexusartig aus. Die normale Tesseraplatte ist zu dünn, um der Entwicklung von Knochenzellen Raum zu bieten. Sobald nur eine geringe tuberkelförmige Wölbung der Tesseraplatten einsetzt, erscheinen Knochenzellen in normaler Gestalt, die Tesserae färben sich dunkel wie die Tuberkel. Nur die Spitze des Tuberkels nimmt den Charakter von Mesodentin an; die Tesserae entsprechen etwa dem Sockel der Tuberkel unterhalb der Randzacken des Tuberkels, sie sind daher knöcherne Gebilde, deren Form entscheidend durch das Porenkanalsystem beeinflußt wird. Sie stellen ein Stadium beginnender Reduktion dar; ihr Verlust würde zu einer Panzeroberfläche mit isolierten Tuberkeln führen. Die Tuberkel gehören phyletisch aber keiner sekundären Generation an, da sie Überreste der alten geschlossenen Dentindecke sind, die im Ventralpanzer noch keine Diffenrenzierung in Tuberkel und Tesserae aufweist.

Das in der Vorderhälfte des Panzers wohlerhaltene Endoskelett ist überwiegend in Gestalt von Knochenröhren erhalten, die Gefäße und Nerven umhüllen. Es schmiegt sich mit einer dünnen Lage der Unterseite der als typisches Isopedin entwickelten Unterschicht des Exoskelettes an. Das Isopedin ist verknöchertes, sehr deutlich und regelmäßig gebündeltes Bindegewebe (Gross 1956). Von ihm hebt sich das Endoskelett schon durch seine kräftig braune Farbe ab; es besteht aus echtem Knochen wie die Mittelschicht und die Tuberkel, nur sind seine Knochenzellen sehr typisch langgestreckt und spindelförmig, ähnlich den Knochenzellen in der Unterschicht der Antiarchi und Rhipidistia. Zwischen Endoskelett-Knochen und Exoskelett-Knochen besteht kein histologischer Unterschied. Isopedin und die Mittelschicht sind im histologischen Aufbau viel verschiedener als das Endoskelett und die Mittelschicht.

Die Porenkanalsysteme der Osteostraci und der Rhipidistia sind sicher homologe Bildungen. Sie sind grundsätzlich an die Oberschicht gebunden, aber nicht unbedingt an eine Dentinschicht, denn bei *Tremastaspis* und *Dartmuthia* ist das Porenkanalsystem von Knochen umgeben. Das Porenkanalsystem kann demnach nicht als mehr oder weniger zufällige Aussparung bei der Verbindung von Hautzähnen bezw. Lepidmorien zu einer geschlossenen Schicht angesehen werden. Dagegen spricht auch der hohe Grad der Differenziertheit dieses Kanalsystems, die Entwicklung von Siebplatten und das Auftreten bei den verschiedensten Gruppen der Agnathen und Fische. Die Einbeziehung der Sinneslinien (Osteostraci) und Grübchenlinien (pitlines der Rhipidistia und Dipteriden) in das Porenkanalsystem weist auf oberflächennahe Sinnesorgane, deren Innervierung anscheinend so diffus war wie das unserer Hautsinnesorgane.

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Are the Accessory Branchial Organs in Characidean Fishes Modified Fifth Gills or Rudimentary Ultimobranchial Bodies?

by

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(Received June 1960)

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Introduction

Accessory branchial organs (Pharyngeal pockets of LAGLER & KRAATZ 1945; Accessorische Branchial Organe of SAGEMEHL 1885, 1887; Accessorische Kiemenorgane of HYRTL 1855) have been known for a long time in fishes. A general survey of the investigations of this structure has been published by RAUTHER (1910). Many types of accessory branchial organs have been described (cf. GEGENBAUR 1901).

KNER (1861) discovered accessory branchial organs in herbivorous characids (*Curimatus, Caenotropus* and *Hemiodus*). SAGEMEHL (1885, 1887) found them also in other herbivorous characids (*Prochilodus* and *Citharinus*). LAGLER & KRAATZ (1945) examined several characids but failed to find any structure of this kind.

Kner described the structure as a cone-formed or sometimes spiral-formed pocket, ending in a blind sac and situated in the posterior part of the gill chamber. On the inside of the pocket there are papillae formed from the lining of the pocket. Sagemehl found that the pockets are formed from "dem oberen

Rande der letzten Kiemenspalte". The papillae were said to be modified fifth gills, a structure nowadays present only in selachians and dipnoans.

This paper is an attempt to find an answer to the questions concerning the homology, function and evolution of the accessory branchial organs in *Characidae* by means of an examination of their ontogeny. Such work has not hitherto been published.

Material and methods

The material consists partially of African characids brought to Stockholm by the two Swedish expeditions to Gambia in 1931 and 1950 respectively, and partially of South American characids reared in Stockholm.

The material is as follows, grouped according to BERG (1958) and modified according to BERTMAR (1960):

CYPRINIFORMES (OSTARIOPHYSI)

Characinoidei

Characidae

Alestes nurse	9	series,	7.7—22 mm
Citharinus citharus	4	„	10—14.5 „
Distichodus brevipinnis	5	„	10—62.5 „
Distichodus rostratus	4	„	14—16 „
Hemigrammus ocellifer	17	„	2.5—6.8 „
Hepsetus odoë	70	„	egg—45 „
Hyphessobrycon innesi	1	„	17 „
Hyphessobrycon roceus	6	„	2.9—3.8 „
Nannaethiops unitaeniatus	1	„	8 „
Nannocharax ansorgei	1	„	15 „
Nannostomus aripirangensis	16	„	1.5—4.1 „

Fixation of the South American species was performed according to BOUIN, SMITH (1912) and BODIAN (ROMEIS 1943). The African material was fixed according to Bouin and Smith.

The material was embedded in paraffin and sectioned in series. As a rule the thickness of the sections was 4—8 microns.

The preparations were stained in Azan-Mallory (HEIDENHAIN), Foot's modification of Masson's tricromestaining, chromealun-haematoxylin (GOMORI) and BODIAN (ROMEIS 1943).

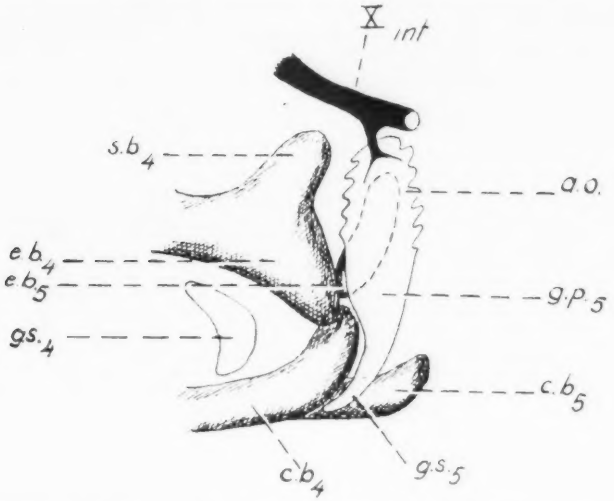

Fig. 1. *Citharinus citharus*, 10 mm. Reconstruction of the position of the left accessory branchial organ, medial view. 83.3 ×.

Ontogeny

CITHARINUS CITHARUS (GEOFFROY)

The position and gross anatomy of the adult accessory branchial organs in *Citharinus* were described and figured by SAGEMEHL (1885, 1887). They have the shape of a dorsoventral pocket of about 8 mm in length, situated medially to the operculum and the fourth epibranchial. There is nothing more to be added than that the organ is situated between the pharynx and the oesophagus, and that the entrance canal of the structure lies medially to the fifth epibranchial, not to the fourth ceratobranchial (Fig. 1).

According to Sagemehl each pocket is kept open by two rows of gill rakers, enlarged and distally sometimes split up into several ends. Further, the wall is lined with leaf-like papillae ("Läppchen") (cf. Figs. 1, 3). Each papilla is constituted by striated musculature and contains a canal entering the pocket. The canals are stiffened by thin cartilage rods. The character of the epithelium was not determined. As the papillae have the same position as a fifth gill Sagemehl suggested that they were modified gill filaments of the fifth branchial arch. This investigation of the ontogeny reveals, however, that Sagemehl's theory is incorrect.

The ontogeny of the accessory branchial organs gives us a new idea of their homology and even of their function. The organs (Figs. 1—3, a.o.) form as an enlargement of the dorsal portion of the fifth gill pouches ($g.p._5$). Ventrally these pouches push out from the endodermal lining of the pharynx and meet the

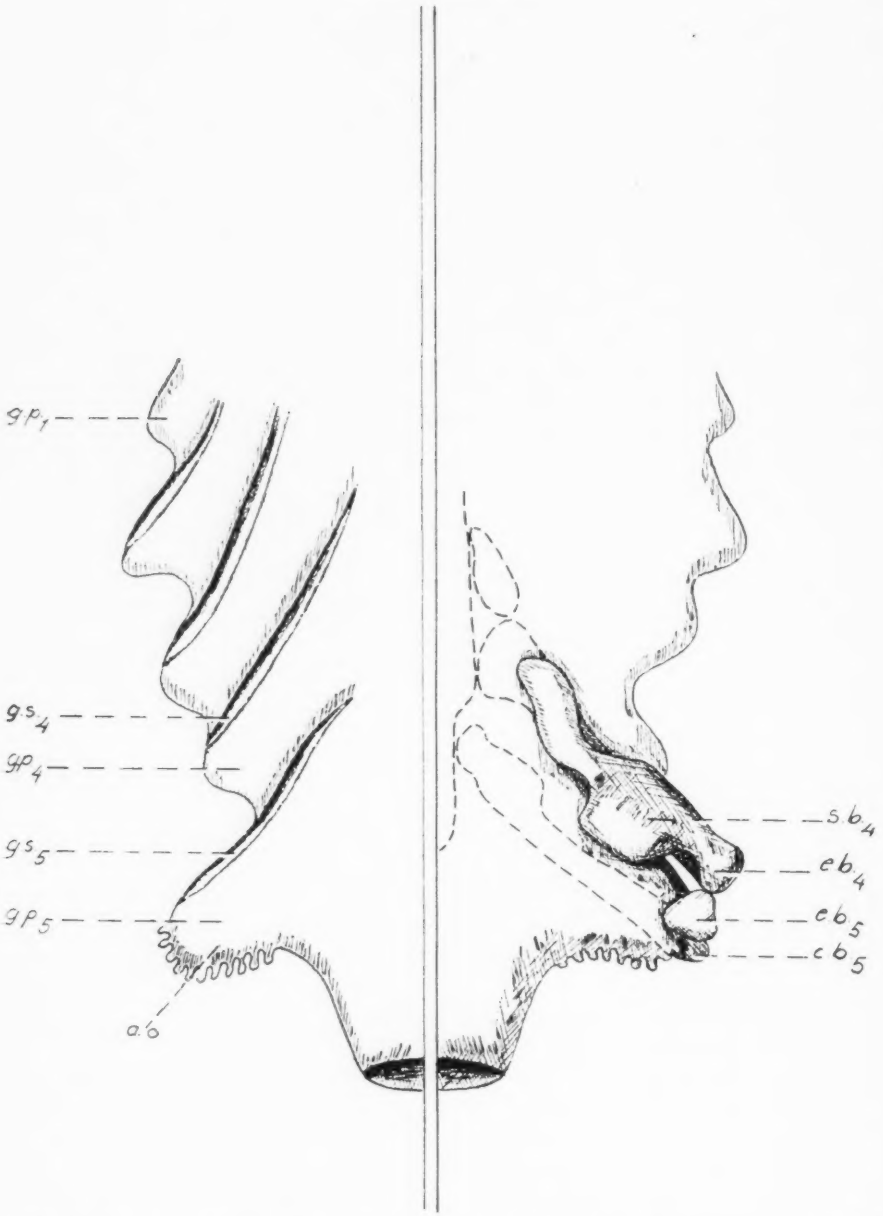

Fig. 2. *Citharinus citharus,* 10 mm. Reconstruction of the position of the accessory branchial organs. Left, ventral view, brancial arches omitted; right, dorsal view. 83.3 ×.

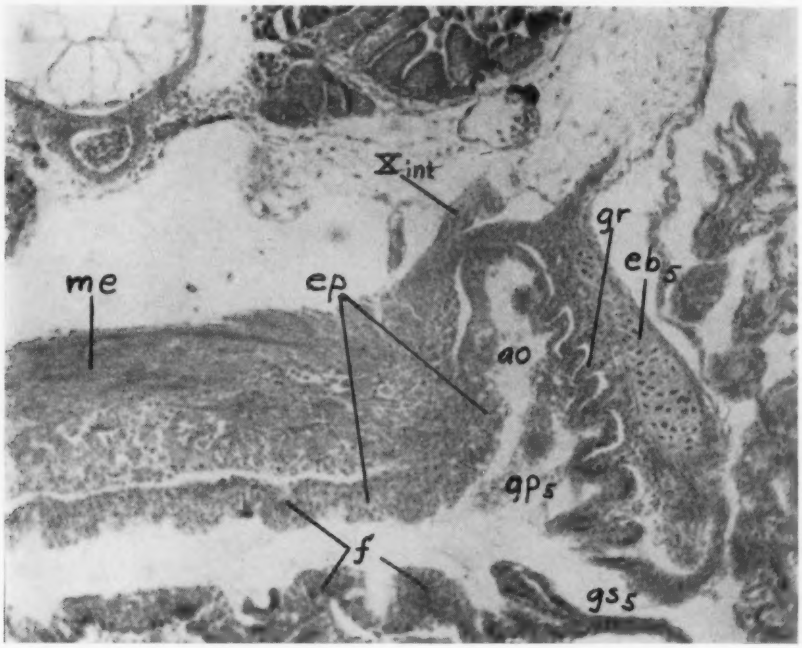

Fig. 3. *Citharinus citharus,* 10 mm. Transverse section through the left side of the skull, on a level with the accessory branchial organ, the fifth gill pouch and the fifth gill slit. 100 ×.

fifth ectodermal visceral grooves, forming a fifth gill slit ($g.s._5$). This gill slit is accordingly shorter than the others.

The ontogeny also shows that long gill rakers (Fig. 3 g.r.) grow out and protrude into the fifth gill pouches and into the accessory branchial organs. They are situated on the medial margin of the fifth epibranchial ($e.b._5$) and on the dorsal side of the fourth ceratobranchial.

However, no fifth gills are formed. The posterior gills belong to the fourth branchial arches. The leaf-like papillae ("Läppchen") are not modified gill filaments as Sagemehl suggested. It is obvious that they are instead endodermal in origin and modified from pharyngeal folds.

The accessory branchial organs were said above to be situated at the border of the pharynx and the oesophagus. Morphologically they belong to the pharynx, as can be expected from their formation from a gill pouch. Anatomically and histologically, however, they also belong to the oesophagus: (1) the striated musculature of the oesophagus surrounds them (Fig. 3, me.); (2) the longitudinal folds of the oesophagus reach the region of the accessory branchial organs (f.); (3) the stratified, non-vascular mucous epithelium of the oesophagus is also present in the accessory branchial organs (ep.).

The ontogeny shows that the papillae form through modification of the small

folds of the posterior pharyngeal wall. These folds (papillae) are built in the same way as those of the anterior part of the oesophagus (but are smaller), viz. a stratified, non-vascular mucous epithelium, a connective tissue layer (lamina propria mucosae) and, outermost, a longitudinal and a circular muscle layer (cf. Fig. 4). The presence of striated musculature and connective tissue in the papillae, described by Sagemehl, is thus explained.

Sagemehl aslo described cartilage rods stiffening the papillae. These rods are formed late in the ontogeny (they are only blastemal in a 15 mm specimen) and have obviously nothing to do with gill rays.

The accessory branchial organs are innervated by the intestinal ramus of the vagal nerves (Figs. 2, 4, $X_{int.}$) and the blood supply comes from the dorsal aortas. Thus, also the innervation and blood supply support the interpretation of the accessory branchial organs as structures non-homologous with modified fifth gills.

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DISTICHODUS BREVIPINNIS (GÜNTHER), D. ROSTRATUS (GÜNTHER), NANNOCHARAX ANSORGEI (BOULENGER), NANNAETHIOPS UNITAENIATUS (GÜNTHER) AND ALESTES NURSE (RÜPPEL)

All these African characids have a rudimentary accessory branchial organ on each side. As in *Citharinus* each organ consists of a dorsal extension of the fifth gill pouch, a sac, lined with a stratified, non-vascular, mucous epithelium and stiffened by gill rakers, protruding into its lumen. Papillae push out from the sac. The innervation and blood supply are also the same.

However, the organs are much smaller in these fishes than in *Citharinus* (Fig. 4). The pockets are shorter, the gill rakers and papillae smaller.

Hence, the accessory branchial organs in these fishes are rudimentary and seem to represent a first step in the evolution towards the well differentiated type in *Citharinus*.

Accessory branchial organs have not been traced in South American characids. The material available for this investigation consisted, however, essentially of rather small embryos (cf. p. 152).

Function

RESPIRATORY

The function of the accessory branchial organs in *Citharinus* is discussed by SAGEMEHL (1887). "Welcher Art das von aussen aufgenommene Medium sei, ob Wasser oder Luft, kann mit Sicherheit nicht entschieden werden, da keine einzige darauf bezügliche Angabe vorliegt." But when compared with other fishes having accessory branchial organs Sagemehl suggested that the characidean structure

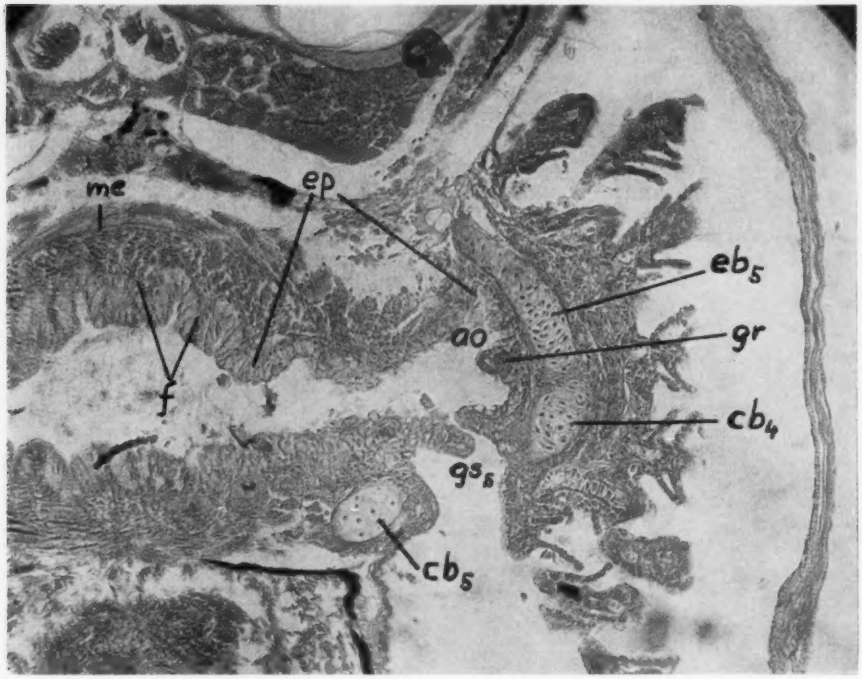

Fig. 4. *Alestes nurse*, 13 mm. Transverse section through the left side of the skull, on a level with the accessory branchial organ, the fifth gill pouch and slit. 100 ×.

was a respiratory organ. This conception was accepted by RAUTHER (1910). The latter did not, however, make any investigation of his own of characids.

Other fishes with accessory branchial organs have been described from *Anabantidae, Ophiocephalidae, Periophtalmidae, Amphiopnoidae, Scaridae, Osteoglossidae, Clupeidae, Alepocephalidae* and *Siluroidae*. The organs have a different morphology (GEGENBAUR 1901; RAUTHER 1910; and others) but are nevertheless said to be homologous and the function respiratory.

Later, however, LAGLER & KRAATZ (1945) and KAPPOOR (1954) proposed that the accessory branchial organs in *Dorosoma cepedianum* (Lasneur) and *Chanos chanos* (Forskal), respectively, were accessory to the digestive tract. These authors examined the histology of adult organs and found that the lining of the organs is mucous and non-vascular. No gills could be traced within them. In these fishes the organs are formed from the roof of the posterior part of the pharynx. Each consists of a pharyngeal pocket, ending in a blind sac.

The position, ontogeny and morphology of the accessory branchial organs in *Dorosoma* and *Chanos* are about the same as in *Characidae*, and the structures therefore seem to be homologous. Whether they are homologous with the acces-

sory branchial organs in the other families mentioned seems doubtful, however. On this point we need ontogenetical investigations.

The ontogeny of the characidean accessory branchial organs has made it reasonable to assume that the organs are n o t accessory to the respiratory system. The reasons are as follows:

(1) The epithelial lining of the lumen is mucous, not vascular;
(2) The leaf-like papillae are modified endodermal folds of the pharynx (oesophagus), not ectodermal gill filaments;
(3) The organs are innervated from the intestinal ramus of the vagal nerves, not from any branchial ramus;
(4) The organs get their blood supply from the dorsal aorta, not from any branchial artery.

GLANDULAR

As is well-known, gill pouches have areas of epithelium which are easily adaptable to glandular development. The teleostean pseudobranchie for example often have an endocrine function. Other glands are derived from the endodermal epithelium of the gill pouches in all gnathostome classes (VAN BEMMELEN 1885—87; LEYDIG 1853; DE MEURON 1886; MAURER 1888, 1898, 1899, 1913, 1917; and others). These glands are formed by thickenings of gill pouch epithelium at either dorsal or ventral borders of the pouches — thickenings which later separate from the epithelium to become buried in the throat region of the adult (Fig. 5).

In most jawed vertebrates small glandular epithelial bodies arise in the neighbourhood of the last pair of gill pouches. Hence, they are termed u l t i m o b r a n c h i a l b o d i e s (Postbranchiale Körper of MAURER 1888, Supraperikardialkörper of VAN BEMMELEN 1885, or glandes thyroides accessoires of DE MEURON 1886). They are sometimes clearly seen to be derivatives of the last (fifth) gill pouches (Fig. 5). Usually they form small clusters of glandular follicles, tubes, or cell strands.

Ultimobranchial bodies have been found in selachians and holocephalians (VAN BEMMELEN 1885) but not in teleostomian fishes. Of the latter fishes, only a few have been investigated in this connection, viz. *Salmo, Esox, Cottus, Gasterosteus, Leuciscus, Barbus* and *Cyprinus* (MAURER 1886, 1888). None of these species had any traces of ultimobranchial bodies. In sharks van Bemmelen found that the ultimobranchial bodies form as an outgrowth of the posterior margin of the fifth gill pouches (Fig. 5). He therefore supposed them to represent vestigial sixth gill pouches. They form early and become cut off from the gill pouches but they stay in this region. Histologically they are said to conform with the thyroid. This is also valid for mammals but not for amphibians (MAURER 1888). In mammals they are secondarily incorporated in the mass of the thyroid tissue, but in lower vertebrates they are free.

Little is known of the function of the ultimobranchial bodies. MAURER (1913)

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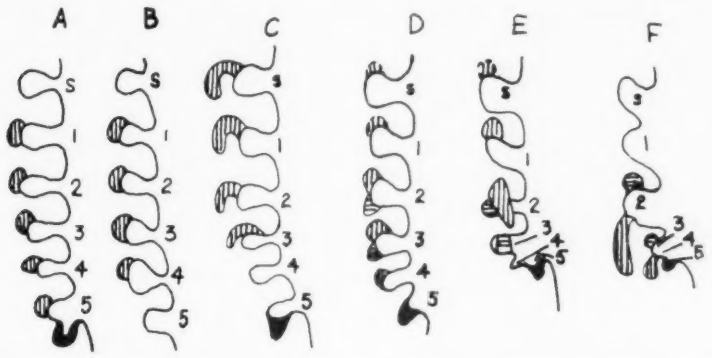

Fig. 5. Diagrams of the gill pouches of the left side of the pharynx, to show the derivation of thymus, parathyroid, and ultimobranchial bodies. A, characids; B, other teleosts; C, sharks; D, urodeles; E, lizards; F, typical mammals. The dorsal part of each gill pouch is, for the purposes of the diagram, at the upper side. Broken outline, variable thymus derivates; vertical hatching, thymus; horizontal hatching, parathyroid; solid black, ultimobranchial body. s, spiracular pouch; 1—5, gill pouches. All types except A are from MAURER (1899, Figs. 5, 6, 8) and ROMER (1950, Fig. 203), partly modified.

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suggests that they are endocrine and that "bei Schwund der respiratorischen Kiemenspalten doch gewisse Epithelbezirke im Dienste der genannten (endocrine) Funktion als Epithelkörperchen erhalten bleiben".

The accessory branchial organs in characidean fishes are also formed as a dorsal outgrowth of the fifth gill pouches (Figs. 1—5) and consist of glandular follicles and tubes (papillae). It is then reasonable to suggest that the characidean accessory branchial organs are homologous with the ultimobranchial bodies in sharks and other gnathostomes.

The difficulty is, however, (1) that the ultimobranchial bodies in other gnathostomes close off from the gill pouches, whereas the accessory branchial organs in *Characidae* do not. (2) The ultimobranchial bodies are endocrine, the accessory branchial organs exocrine: the ultimobranchial bodies discharge their secretion into the interstitial fluid or the blood vessels, the many unicellular glandular cells of the characidean accessory branchial organs instead secrete their products in the water washing through from the pharynx.

However, the different function of the two structures need not, of course, be an obstacle to a homologisation. The thyroid gland is also endocrine, although according to MÜLLER (1869) and DOHRN (1886), for instance, it is homologous with the exocrine endostyle in lower chordates.

Concerning the first difficulty above it then seems reasonable to suggest that the exocrine accessory branchial organs in *Characidae* represent a first step in evolution towards the endocrine ultimobranchial bodies in gnathostomes. This theory is also supported by the fact that the characidean skull shows many primitive characters (BERTMAR 1959, 1960).

As a parallel it might be mentioned that the ciliated and glandular endostyle channel in lower chordates strains food particles out of the water current carried back to the intestine. In *Ammocoetes* the groove is only vestigial and at metamorphosis it closes off from the gut and breaks up into a series of follicles, secreting a thyroid hormone.

The accessory branchial organs in characids also seem to strain food particles: there are long gill rakers protruding into the organs (p. 155) which probably attract a sample of food from the respiratory water. The food and the water can then be treated by the glandular epithelium of the organs in order to get information of their quality. In sharks and in tetrapods the embryonal accessory branchial organs, like the exocrine endostyle in *Ammocoetes,* close off from the pharynx and become the endocrine ultimobranchial bodies in the adult (cf. Fig. 5).

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Summary and conclusions

1. Paired accessory branchial organs constitute a structure associated with the medial side of the fifth epibranchials in the African characids *Citharinus* (Figs. 1—3), *Alestes* (Fig. 4), *Distichodus, Nannocharax* and *Nannaethiops. Alestes* is carnivorous, the others herbivorous.
2. The organs are lacking in *Hepsetus* (*Sarcodaces*) and the South American characids *Hemigrammus, Hyphessobrycon* and *Nannostomus.*
3. The organs are most differentiated in *Citharinus* (Figs. 1—3). They consist of a dorsoventral pocket (sac) protruding from the dorsal wall of the fifth gill pouches and are lined with mucous, non-vascular epithelium. The leaf-like papillae extending from the pocket are not modified gills of the fifth arch as was suggested by Sagemehl and others. Ontogeny, innervation and blood supply show that they are instead of endodermal origin and are formed through modification of pharyngeal folds of the type present in oesophagus.
4. Function is glandular (exocrine), not respiratory as was suggested before.
5. Homology with the pharyngeal pockets in *Elopidae* and *Chanidae* seems probable.
6. Evolution appears to be the result of an increased dorsal growth of the fifth gill pouches, beginning with a rudimentary type present in *Alestes, Distichodus, Nannocharax* and *Nannaethiops,* via a more differentiated type in *Citharinus,* and ending in the ultimobranchial bodies in sharks and tretrapods (Fig. 5).

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Abbreviations

a.o. accessory branchial organ
c.b. ceratobranchial
e.b. epibranchial
ep. epithelium of oesophagus
f. longitudinal fold of oesophagus
g.p. gill pouch
g.r. gill ray
g.s. gill slit
m.e. striated musculature of oesophagus
oe. oesophagus
ph. pharynx
s. spiracular pouch
V nervus vagus
$X_{int.}$ intestinal ramus of nervus vagus.
1—5 gill pouches

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On the structure of the laterosensory System in Sharks and Rays

by

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(Received July, 1960)

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In elaborating the problems of the origin of ancient vertebrates A. Severtzoff and his pupils devoted considerable attention to studying the peculiarities in the structure of the different organ systems of the *Elasmobranchii,* representatives of the oldest subclass of the *Gnathostomata* (A. SEVERTZOFF, 1898, 1899, 1923, 1925, 1931, 1934; A. SEVERTZOFF and N. DISLER, 1924; M. WOSKOBOINIKOFF, 1914; B. MATVEIEV, 1915, 1923, 1925; S. KRYŽANOVSKIJ, 1917; S. EMELIANOV, 1926; O. BELOBORODOVA, 1928; A. RINDSÜNSKY, 1929, 1939). These works are of essential importance to the solution of the problem of the primary structure of ancient fishes and their phylogenesis. In particular, in order to elucidate the genetic relations between the rays and other groups of ancient fishes, A. Severtzoff investigated the development of sharks and rays. In addition to investigating the development of the external fetal shapes of these fishes (A. SEVERTZOFF, 1931), the structure of the visceral apparatus was studied by A. KRIVETSKY (1917, 1925) and N. DISLER (1927-b), as well as the lateral-line sense organs by N. DISLER (1927-a, 1941, 1953).

In summarizing the works of his pupils, as well as his own numerous investigations into the structure of the *Elasmobranchii,* A. SEVERTZOFF (1931) arrived at the conclusion that in origin rays were closely related to sharks. We deem it necessary to recall these works of the morphologists of the A. Severzoff school because the extensive and carefully analyzed factual material, on which the phylogenetic concepts of these investigators are based, is ignored by the contemporary morphologists. Underestimation of the importance of A. Severtzoff's research in the evolution of the ancient vertebrates gives rise to a number of erroneous concepts. For example, an idea is now current among the morphologists of the

Swedish school that the structure of the lateral-line sense organs of rays is similar to that of the *Holocephalians* and *Arthrodires* and has little in common with that of the other *Gnathostomata,* including the sharks. This wrong conclusion is based on N. Holmgren's inaccurate reconstruction of the head of the embryo of the Torpedo occellata (Fig. 1 A). The aforesaid reconstruction published by N. Holmgren (1942) was later reproduced in E. Stensiö's monograph (1947) and reincorporated in the work of N. Holmgren and T. Pehrson (1949). The data on the presumable resemblance of the structure of the organs of the lateral-line system on the cheek of the *Holocephalians* to that of the rays are repeated, with reference made to N. Holmgren, in Ch. Devillers' investigation (1950).

Before proceeding to an analysis of N. Holmgren's reconstruction it will be observed that, as regards homologizing the cutaneous sense organs in the cheek of the *Elasmobranchii,* I adhere to the concepts well-grounded as a result of the analysis of the factual data furnished by the works of J. Ewart (1892), J. Ewart and J. Mitchell (1892), E. Allis (1901, 1923, 1934), S. Johnson (1917), and G. Ruud (1920).

E. Allis (1934) notes that among the *Elasmobranchii* the cheek lines are most fully pronounced in the present-day representative of ancient sharks, the *Chlamydoselachus anguineus.* In this shark E. Allis notes jugal-oralomandibular and spiracular-gular (Preoperculo-mandibular) lines. In this shark the neuromasts are located partly in canals and partly in deep dermal fissures.

Existence of the 2nd jugal line (N. Holmgren, 1942) in ancient fishes is doubtful because no evidence of existence of such a line was found in either representatives of the *Chlamydoselachus* (E. Allis, 1923) of embryos of the *Heptanchus* (N. Disler, 1941).

In pentabranchiate sharks the jugal (hyomandibular after J. Ewart 1892) and oralomandibular (mandibular after J. Ewart) lines have the form of canals, while the spiracular-gular (preoperculo-mandibular) line is represented as a series of open neuromasts—follicles.

According to E. Allis (1934), the rays have in the area in question two lines —jugal (hyomandibular 1, 2, 3, 4, 5, 6 after Ewart and Mitchell 1892) and oralomandibular (hyomandibular 7 after Ewart and Mitchell, 1892). E. Allis assumes the possibility of the existence of the spiracular-gular (preoperculo-mandibular) line in rays, this line being represented in the pentabranchiate sharks by a series of open neuromasts, but not found in rays as yet.

In examining the general inferences drawn from the investigations conducted by J. Ewart, J. Mitchell and E. Allis regarding the sense organs of the lateral-line system of the *Elasmobranchii* it should be noted that these scientists stressed the common structure of these organs in sharks and rays, something that has found its reflection in the diagram (Fig. 1 C) accompanying the work of J. Ewart and J. Mitchell (1892) and latter reproduced in E. Allis' work (1934).

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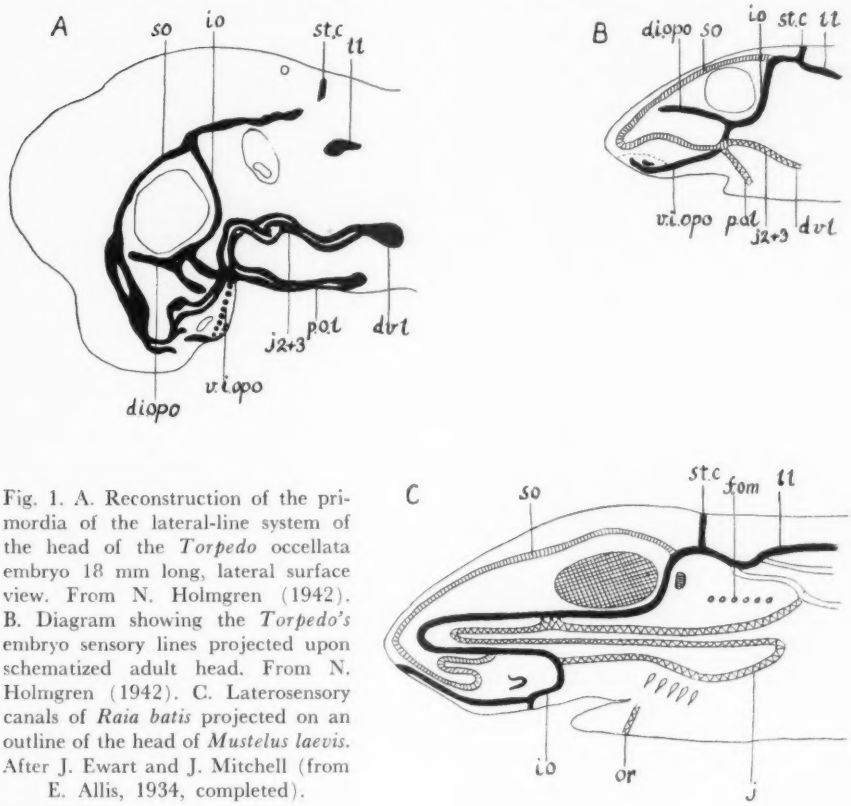

Fig. 1. A. Reconstruction of the primordia of the lateral-line system of the head of the *Torpedo* occellata embryo 18 mm long, lateral surface view. From N. Holmgren (1942). B. Diagram showing the *Torpedo's* embryo sensory lines projected upon schematized adult head. From N. Holmgren (1942). C. Laterosensory canals of *Raia batis* projected on an outline of the head of *Mustelus laevis*. After J. Ewart and J. Mitchell (from E. Allis, 1934, completed).

The materials on the development of the *Torpedo ocellata* and the *Trygon pastinaca* (kindly placed at my disposal for investigation by B. Matveiev) embrace stages close to those described by N. Holmgren (1942) and also make it possible to study the structure of rays at earlier and later stages. In the present report I wish to call attention to the stage of development which in close to the one investigated by N. Holmgren. I investigated the primordia of the lateral-line organs of the *Elasmobranchii,* the Torpedo in particular, by various methods. In addition to studying the primordia on sections and by the method of graphic reconstructions, the distribution of the primordia was studied on the surface of embryos with reflected light and by making preparations of ectoderm removed from different parts of embryonic bodies and their examination in a passing light. The latter method, as is well known, was widely used by G. Ruud (1920) in investigating the development of the primordia of the lateral-line organs in the *Spinax niger*. This method yields good results which make it possible to control the correctness of graphic reconstructions. The study of the structure of the *Torpedo,* embryos, a 21-mm longe one in particular, has shown that Holmgren's re-

construction was really made from a *Torpedo* embryo about 18 mm long, as he had indicated in his work of 1942, and not 12 mm long, as was pointed out in the work of N. Holmgren and T. Pehrson (1949) (the same reconstruction is given in both works but different sizes are cited).

It should be noted that N. Holmgren's work not only ignores the methods of investigation developed by G. Ruud but also completely fails to reflect the results of her observations showing the possibility of distinguishing in the ectoderm of the embryos the position of the placodes (from very early stages of their development) from which the lines of neuromasts and later the ampullar fields—ectodermal thickenings giving rise to the primordia of the ampullae—are formed. Thus in N. Holmgren's reconstruction the primordium of the lateral-line organs in the *Torpedo* embryo in the area anterior to and below the eye is shown greatly dilated with a lumen in the middle (Fig. 1 A, so). As a matter of fact only the internal part of this dilatation is the supraorbital placode from which the line of neuromasts is formed, the external one belonging to the ampullar field located here parallel to the supraorbital line (Fig. 2 A, a, f.sor).

In the area lying anteriorly to the nasal aperture the N. Holmgren's reconstruction shows two short branches running downward and backward from the supraorbital line.

Farther on the primordia line in the reconstruction is divided in two parallel-running lines above the olfactory opening. These lines join again in their posterior parts. Indeed in this area of embryo we find the inferior division of the supraorbital line and the ampullar field parallel to it. The posterior end of the supraorbital line does not join the infraorbital line. The N. Holmgren's reconstruction shows them joined (Fig. 1 A, so, io and Fig. 2 A & B, a_1, f.sor, f.ior). Investigation of the embryos has shown that the "postnasal dorsal branch" of the infraorbital line (Fig. 1 A, diopo), which in N. Holmgren's reconstruction occupies the area below the eye, does not really exist. In this area there are no primordia of neuromasts. The ectoderm shows no signs of structure warranting the assumption of a placode. As a matter of fact, the infraorbital line in the area below the eye forms a small bend directed forward. Then it continues on to the lower surface of the head and runs between the mouth and the nasal aperture (Fig. 2 A and B, f.ior). In the *Torpedo* the rostral part of the infraorbital line (postnasal ventral branch of infraorbital line after N. Holmgren) is an independent primordium (Fig. 2 B, f.ior). N. Holmgren's reconstruction does not reveal this peculiarity in the structure of *Torpedo's* infraorbital line (Fig. A, v.i.opo).

The structure of the lateral-line organs in the cheek of the *Torpedo* embryo is also misrepresented. The thing that is marked as the 2+3 jugal lines in the reconstruction, the lines continuing in the rear into the dorsoventral line and merging in front with the infraorbital line and the anterior ends of the primary-oral line (Fig. 1 A, j2+3, dvl, p.o.l., io) is actually a complex of primordia formed by the jugal line and the adjacent ampullar fields (Fig. 2 A, f.b, C, C_1, C_2).

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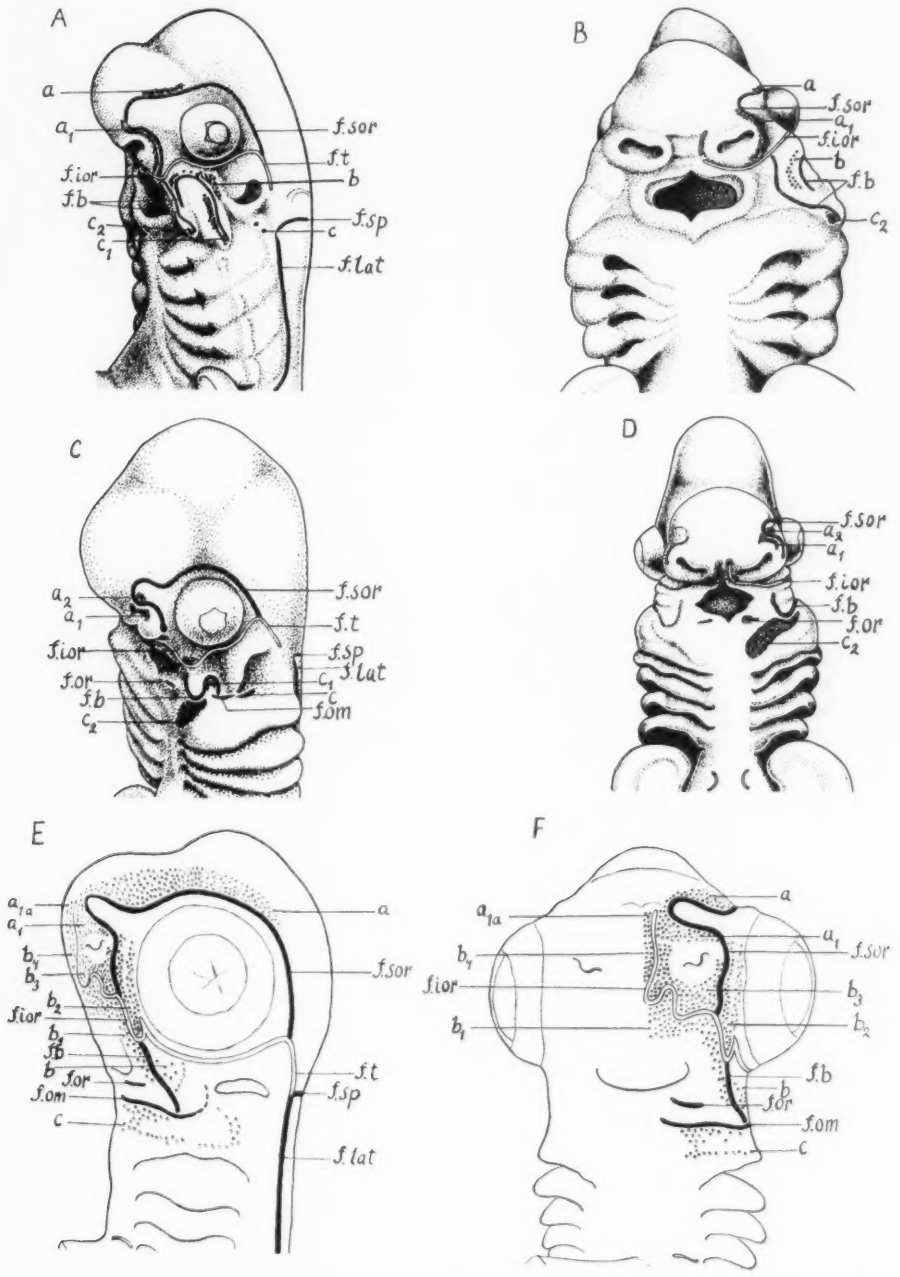

Fig. 2. Heads of ray and shark embryos (External gills removed). A. *Torpedo occellata* 21 mm long; lateral surface view. B. *Torpedo occellata* 21 mm long; ventral view. C. *Trygon pastinaca* 29 mm long; lateral surface view. D. *Trygon pastinaca* 29 mm long; ventral view. E. *Acanthias acanthias* 32 mm long; lateral surface view. F. *Acanthias acanthias* 32 mm long; ventral view.

Owing to the confusion of the neuromast lines and the ampullar fields, the reconstruction fails to convey the structure of the organs also in this area. In particular, this applies to the peculiarity in the structure of the jugal line characteristic of the *Torpedo* and representing two isolated primordia. Of these the upper one is located below the spiraculum as it is shown in Fig. 2 A (f.b). The anterior end of this part of the jugal line curves hook-like and passes on to the ventral surface of the head. Here it ends a little short of reaching the posterior end of the ventral division of the jugal line. At the site of the bend the dorsal part of the jugal line runs some distance behind and parallel to the infraorbital line and does not merge anywhere with it. In this part the noted lines are divided by the ampullar field (Fig. 1 A, B). The ventral division of the jugal line begins posteriorly to the infraorbital line at the point where the posterior end of the supraorbital line approaches this line anteriorly. Despite the representation in the reconstruction, this ventral division of the jugal line adjoins the infraorbital line but does not merge with it (Fig. 1 A, so, io, p.o.l and 2 A and B, f.b, f.ior, f.sor).

There are four ampullar fields on the cheek of the *Torpedo* embryo (Fig. 2 A and B, b, c, c_1, c_2). Three of them adjoin the jugal line (c, c_1, c_2). The latter in combination with the primordia of the neuromasts create in the reconstruction the impression of parallel or merging lines. One of the ampullar fields, weakly differentiated as yet, adjoins the posterior end of the ventral part of the jugal line (c_2). The second one lies along the anterior part of the dorsal division of the jugal line (b). This ampullar field has already broken up into primordia of individual ampullae. This field separates the dorsal division of the jugal line from the infraorbital line. The third ampullar field is located along the posterior part of the dorsal division of the jugal line and adjoins it from below (c_1). Unlike the representation in the reconstruction, the ampullar fields do not merge with the primordia of the neuromast lines anywhere. This applies not only to the fields with already differentiated primordia of ampullae but also to weakly differentiated fields.

N. Holmgren's reconstruction shows behind the spiraculum a pear-shaped placode marked as a main lateral-line (Fig. 1 A, ll). According to my observations, at the corresponding place of the embryo head there is a small ampullar field (the fourth cheek field) from which two spiracular ampullae (Fig. 2 A, c) are differentiated. The lateral line of the body lies above this place. Its anterior part joins the supratemporal line (Fig. 2 A, f. lat and f.sp).

Investigation of the lateral-line sense organs in the *Trygon pastinaca,* a representative of another family, extends our ideas of the peculiarities in the structure of this system of organs in rays.

For comparison we took a *Trygon* embryo 29 mm long at an earlier stage of development than the 21-mm *Torpedo* embryo. There are no essential differences between the two embryos in the position of the supraorbital line relative to the eye and the nasal aperture (Fig. 2 A, c, f.sor).

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It should be observed, however, that the ventral part of the supraorbital line in the *Trygon* is in the process of differentiation: this line has not fully extended as yet. In connection with this the posterior end of the supraorbital line in the area of the nasal aperture of the *Trygon* is relatively farther from the descending part of the infraorbital line than is the case in the *Torpedo* embryo. The embryos differ as to the position of some ampullar fields adjoining supraorbital line of neuromasts. The *Trygon* does not have the ampullar field lying in the front of the eye, outside and along the supraorbital line of the *Torpedo* (Fig. 2 A and C, f.sor, α). At the same time, unlike the *Torpedo,* the ampullar field of the *Trygon* is located in a loop formed by the supraorbital line in front and above the nasal aperture (Fig. 2 A and C, α_2). Outside of this loop of the supraorbital line, between it and the nasal aperture, there is an ampullar field, similar in the embryos compared (Fig. 2 B and D, α_1).

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In the *Trygon* the lower rostral part of the infraorbital line does not form a separate primordium which is characteristic of the structure of this line in the *Torpedo*. In the *Trygon* the ventral division of the infraorbital line continues without interruption into its rostral part. As for the rest, there are no essential differences between the positions of the infraorbital line in the embryos compared (Fig. 2 A, B, C and D, f.ior). In the *Trygon,* as in the *Torpedo,* there is no postnasal dorsal branch of the infraorbital line. Unlike the *Torpedo,* an ampullar field is formed in the *Trygon* somewhat later in the area between the eye and the ventral descending part of the infraorbital line, this field being as yet but slightly in evidence in the 29-mm *Trygon* embryo. The ampullar field is not as yet pronounced in the *Trygon* embryo, this field arising later on the rostral surface of the head along the ventral part of the infraorbital line. The *Torpedo* has no such ampullar field.

In the investigated embryos the structure of the cheek line differs essentially. The *Trygon* has an oralomandibular line which the *Torpedo* does not have (Fig. 2 B and D, f.or).

Unlike the *Torpedo* the jugal line in the *Trygon* is unbroken. Curving like an S the upper part of this line directly passes into the ventral line without breaking, which is characteristic of this line in the *Torpedo* (Fig. 2 A and C, f.b). The jugal line does not merge anywhere with the infraorbital line in both embryos.

Another interesting peculiarity manifests itself in the structure of the cheek lines in the *Trygon*. The posterior end of the dorsal part of the jugal line adjoins in the area of the spiraculum a small line which is primordial in the described stage of development. This spiracular-gular line runs downward from the lower edge of the spiraculum. It travels behind the posterior end of the dorsal part of the jugal line (Fig. 2 C, f.om). The *Torpedo* does not have this spiracular line.

The ampullar field (Fig. 2 A, b) located in the *Torpedo* between the dorsal division of the jugal line and the descending part of the infraorbital line has not yet differentiated in the cheek area of the *Trygon* embryo. The ampullar field

bordering the ventral part of the jugal line posteriorly is much more powerfully developed in the *Trygon* than in the *Torpedo* (Fig. 2 B and D, c_2). The ampullar fields, one of which is located behind the spiraculum and the other one in the curvature of the dorsal part of the jugal line are as yet rudimentary in the *Trygon* embryo. In the *Torpedo* embryo the corresponding fields have already differentiated and given rise to separate ampullae (Fig. 2 A and C, c, c_1). Later, another small oral ampullar field, which the *Torpedo* does not have, differentiates in the *Trygon*.

The comparison of *Torpedo* and *Trygon* embryos shows that, despite the differences in their structure, the entire course of development of these forms denotes their common origin (Disler, 1927 a). At the same time the investigation of rays revealed no morphological peculiarities warranting an assumption that this sup-order of the *Elasmobranchii* is in any way close to the *Holocephalians*. It shall be recalled that, according to N. Holmgren, the similarity between the rays and *Holocephalians* is denoted primarily by their postnasal dorsal branch of the infraorbital line and the merging of the cheek lines with the descending part of the infraorbital line. As has been shown, this presumable similarity arose as a result of the inaccurately made reconstruction. Nevertheless, the question of the origin of rays, raised by N. Holmgren, compels us to turn again to the comparison of the structures of rays and sharks.

To compare with the rays I took a 32-mm embryo of the *Acanthias acanthias* as a representative of the order of sharks (Fig. 2 E and F). The embryo is at a later stage of development than that of the ray embryos. In the shark embryo the growth of placodes—primordia of the neuromast lines is completed, and the ampullar fields have differentiated into separate primordia of ampullae.

The position of the lines on the cheek surface of the head of the forms compared presents the greatest interest. As in the *Trygon,* in the shark embryo a small oralomandibular line of neuromasts is located behind the mouth (Fig. 2 D and F, f.or). Distal to it is the jugal line (f.b). The attention is attracted by the fact that the anterior end of the jugal line in the ray and shark adjoins the infraorbital line (Fig. 2 D and E, f.b, f.ior, f.sor). In this respect the *Trygon* and *Acanthias* are similar. The forms of the jugal line in the shark and ray differ considerably. In the shark it is nearly straight, runs backward from the infraorbital line and ends a little short of the spiracular-gular line. In the ray the jugal line is S-shaped. The shape of the jugal line of the ray indicates that already at an early stage of development this line begins to grow, something that subsequently leads to a shift of the posterior divisions of this line, both the dorsal and ventral, in the caudal direction to the ventral and dorsal surfaces of the pectoral fins. The anterior ends of these fins grow anteriorly and adhere to the lateral surfaces of the head. The middle part of the jugal line shifts in the rostral direction and in the adult ray is located in front of the eye. The fate of the primordium of the jugal line in the shark differs from that of the rays. In

the shark this line continues to differentiate at the point of its origin (DISLER, 1927 a).

The structure of the spiraculo—gular line varies. This line in the Acanthias begins below the spiraculum, then it goes downward, passes behind the jugal line and ends at the inferior surface of the head (Fig. 2 E, F, f.om.). The position of the spiraculo—gular line relative to the spiraculum and the dorsal posterior end of the jugal line denotes the fact that only the uppermost spiracular part of this line is retained in the *Trygon* (Fig. 2 C, f.om.). In the course of the development the spiraculo—gular line of the shark just as the jugal line changes its position but little relative to the spiraculum the first gill cleft and the mouth. In the ray just as in the shark the spiraculo—gular line similarly formed by a number of follicles stretches backward, as it develops, along the dorsal surface of the branchiate apparatus and runs in the area between the spiraculum and the shoulder girdle (Fig. 1 C, f.om.). The dorsal part of the spiraculo—gular line discovered in the *Trygon* confirms the assumpsion voiced by ALLIS (1934) that this line exists in the rays. The *Torpedo* is completely devoid of the oralomandibular and spiraculo—gular lines. The jugal line of the *Torpedo* is divided, as has been shown, into two primordia, while in the shark and the *Trygon* it is represented by a single primordium. At the same time the general position of the parts of the jugal line relative to the mouth, spiraculum and infraorbital line is similar in the *Torpedo* and the *Trygon,* something that speaks in favour of the homology of these lines in rays belonging to different families.

The connection of the dorsal part of the jugal line with the infraorbital line is of a secondary nature (S. GARMAN, 1888; J. EWART and J. MITCHELL, 1892; H. NORRIS, 1932). This connection occurs at late stages of development and is effected by means of secondary canals that connect the cavities of the main canals in which the neuromasts are located in a manner shown in the diagram (Fig. 1 C, io, j).

The homology of the supra- and infraorbital lines in sharks and rays raises no doubts, but their shapes and positions relative to the eye, mouth and nasal aperture show, in addition to similar features, specific features, since the very proportions of the parts of the body, and particularly parts of the head, differ in them. Thus the eyes of the ray are relatively smaller than those of the shark. The nasal apertures of rays are located in close proximity of the mouth, whereas in sharks they are shifted anteriorly. The rostral surface of the shark's head is relatively much larger than that of the ray's head (Fig. 2 B, D, F).

The parts of the supraorbital and especially infraorbital lines located on the rostral surface are relatively larger in the shark embryo than in the rays. A separate formation of the rostral part of the infraorbital line is, as has been noted, specific for the *Torpedo.*

As an assumption, E. ALLIS (1934) notes that the temporal (dorsal part of the infraorbital) line of the rays in the area located between its connection with the

supratemporal and supraorbital lines is innervated by the r. supratemporalis n.X rather than by the r. buccalis n. VII, as is the case in sharks. This observation is subject to verification, especially since the primordium of the temporal line forms in the rays as a continuation of the infraorbital line and does not have a primary connection with the supratemporal primordium (Fig. 2 A and C, f.ior, f.t). In this respect the development of the rays is similar to that of the sharks (S. Johnson, 1917).

In referring to the structure of the ampullar fields it should be noted that in the *Acanthias* embryo there is the big ampullar field situated behind the spiraculo—gular line (Fig. 2 E, c). The spiraculo—gular line in the rays is either absent (the Torpedo) or small (the Trygon). The big ampullar field of the *Acanthias* corresponds to the three ampullar fields in the rays (Fig. 2 A, C, E, c, c_1, c_2). The superior of them (c) adjoining the spiraculum is similar in its position to the superior part of the big ampullar field of the *Acanthias*. The middle and inferior ampullar fields (c_1, c_2) in the ray are situated separately as distinct from the middle and inferior divisions of the big ampullar field of the *Acanthias* (f.b.). The ampullar field (b) joins the anterior part of the jugal line of the *Torpedo* separating this line from the descending division of the infraorbital line. In the Trygon this ampullar field is not differentiated. The ampullar field in the *Torpedo* corresponds to the ampullar field of the *Acanthias* situated above the jugal line (Fig. 2 A, E, b).

In the anterior part of the head, especially on the rostral surface, the ampullar fields in the ray embryos occupy a relatively small area. Unlike the rays, the ampullar primordia in the *Acanthias* cover a considerable part of the ventral surface of the head, especially in the area of the rostrum (Fig. 2 B, D, F, a, a_1, a_{1a}, b_1, b_2, b_3, b_4).

The ecological significance of the morphological differences found in the development of sharks and rays is still unclear. Cumulative observations on the behaviour of the embryos, representatives of different families of rays and sharks, will subsequently help to disclose the adaptive purport in the structure of these forms.

The analysed material relating to the structure of the sense organs of the lateral-line system of the *Torpedo, Trygon* and *Acanthias* embryos supplements and renders more exact the former observations on the development of the body shape and branchiate apparatus of the representatives of various orders of the *Elasmobranchii* (N. Disler, 1927 a, b; A. Severtzoff, 1931). The accumulated facts denote that the features of the structure of the shark-like ancestors recur in the development of rays, but that they recur differently (the similar features and differences in structure were shown in the description of the ray and shark embryos). It is here that we should look for the reflection of the peculiarities of the environment to which the structure of the developing embryos of different species is adapted.

The analysis of the reconstruction of the head of the 18-mm *Torpedo* embryo has shown that N. Holmgren took into consideration insufficiently the specificity of the primordia of Lorenzini ampullae (ampullar fields) and of the placodes from which the neuromasts (sensory lines) are formed.

The reconstruction shows a non-existent postnasal dorsal branch of the infraorbital line. In the reconstruction the dorsal and ventral divisions of the jugal line and the adjoining ampullar fields appear merged not only with one another but also with the infraorbital line, which, as has been shown, is at variance with the actual structure of these organs.

N. Holmgren's assertion of the structural similarity of the lateral-line organs in rays and *Holocephalians* is not justified.

The scheme proposed by N. Holmgren to illustrate the location of the lateral-line sense organs on the head of rays is incorrect (Fig. 1 B). It is based on the erroneous reconstruction of the head of the *Torpedo* embryo analysed above (Fig. 1 A). The J. EWART and J. MITCHELL scheme (1892) reproduced in E. ALLIS' work (1934) retains its full significance (Fig. 1 C). It makes it possible to picture in a simple form the real relationships in the location of the lateral-line organs of sharks and rays.

The study of the *Elasmobranchii,* the sense organs of the lateral-line system in particular, bespeaks a genetic relation between sharks and rays. Thus the modern data relating to the development of the representatives of ancient groups of fishes confirm the correctness of the inferences drawn by A. Severtzoff as regards the phylogenesis of the *Elasmobranchii.*

Designations

Figure 1.

diopo postnasal dorsal branch of infraorbital line
dvl dorsoventral lateral line
f.om spiracular—gular (prеoperculo—mandibular) line
io infraorbital line
j jugal line
j 2+3 2nd 3rd jugal line
ll main lateral line
or oral line
p.o.l. primary oral line
so supraorbital line
st.c supratemporal line
v.l.opo postnasal ventral branch of infraorbital line

Figure 2.

a,a_1,a_{1a},a_2, ampullae of Lorenzini primordium (ampullar fields), supplied by the r. ophtalmicus super—ficialis n. YII
b,b_1,b_2,b_3,b_4 ampullae of Lorenzini primordium (ampullar fields), supplied by the r. buccalis n. YII
c,c_1,c_2, ampullae of Lorenzini primordium (ampullar fields), supplied by the r. mandibularis externus n. YII
f.b jugal line
f.ior infraorbital line
f.lat main lateral line

f.o.m. spiracular—gular (preoperculo—mandibular) line
f.or oralomandibular line
f.sor supraorbital line
f.sp supratemporal line
f.t temporal line

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On the Histological Differentiation of the Larvae of Pisione remota *(Pisionidae, Polychaeta)*

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VOL. 42 1961

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1. Introduction

In the last decades several papers have been published dealing with the small and aberrant polychaete family Pisionidae. The small-sized, slender members of this family inhabit sandy areas in shallow waters. Some of the known species live in the intertidal zone. Even when a number of different species live in a restricted area, each species inhabits its special type of sand.

The affinities of the family are uncertain. A scheme of the several attempts to connect the pisionids to other polychaete families is seen in *Table 1*.

Table 1. *The different attempts to connect the family Pisionidae to other polychaete families.*

	Aphrodi-tidae	Nephthy-didae	Phyllodo-cidae	Glyce-ridae	Hesio-nidae	Syllidae
Grube (1857)			×	×	×	
Levinsen (1887)	×					
Ehlers (1901)	×	×			×	×
Southern (1914)	×					
Hartman (1939)	×				×	
Aiyar and Alikunhi (1940)			×	×		
Alikunhi (1950)		×	×	×		
Banse (1956)	×	×				

The members of the Pisionidae have a highly specialized type of reproduction including a copulation process (Aiyar and Alikunhi 1940; Alikunhi 1950). The large spermatozoa are non-motile. They undergo a metamorphosis. In the body of the male they are spindle-shaped and provided with a short flagellum. In the receptaculum seminis of the female they are spherical with a circlet of 5—8 stiff processes. The copulation organ consists partly of the modified ventral cirrus of the parapodium, partly of an elongated protrusible organ, which is a differentiation around the efferent duct of the sperm sack.

The anterior end of the pisionids is highly modified with the prostomium fused with the buccal segment and more or less reduced (Fig. 1). The elongate brain projects as two lobes into the third or fourth setigerous segment (Southern 1914; Siewing 1952). The parapodia of the buccal segment form the dorsal part of the anterior end. They are provided with a pair of strong acicula which possibly take part in the decomposition of the food (Siewing l.c.). The acicula represent the rudiment of the buccal parapodia. Two long cirriform cirri project

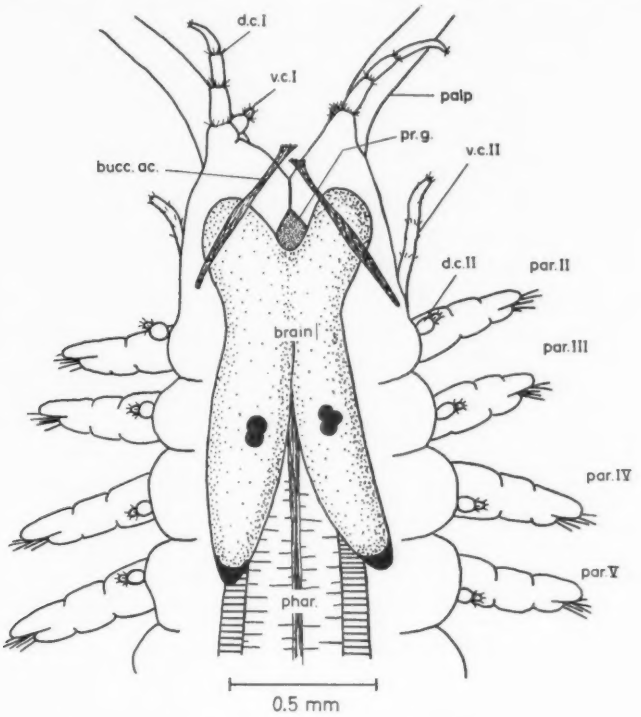

Fig. 1. The anterior end of *Pisione remota* in adult condition.

from the dorsal anterior end of the parapodial bases. Another pair of flask-shaped cirri are attached to the ventral inner part of the long cirri. A pair of large slender palps occupies the ventral part of the anterior end. EHLERS (1901) and HARTMAN (1939) are of the opinion that these appendages correspond to the buccal cirri of the polynoids, but SIEWING, who has studied their innervation, was able to show that they are true palps.

BANSE (1956) has recently given a brief description of the morphology of the larvae belonging to the species *Pisione remota*. Some notes about the trochophore and metamorphosed bottom stages of *Pisionidens indica* are found in the paper of AIYAR and ALIKUNHI (l.c.).

The pisionid trochophore and the metatrochophore stages have a close resemblance to the corresponding stages of polynoid larvae. As the pelagic larvae have no special modifications in the anterior end, it is obvious that these occur during the metamorphosis at the end of the pelagic stage. When the present writer began to collect developmental stages of *Pisione remota* it was primarily for the purpose of studying the histological differentiation of the cerebral region. Secondarily it was his intention to compare the structures of the larvae with those

of larvae belonging to other errant polychaete families in an attempt to solve the affinities of the family Pisionidae.

2. Material and Methods

The material was collected at the Marine Biological Station, Kristineberg, Fiskebäckskil, during the summers of 1959 and 1960.

Pisione remota is abundant on bottoms with fine sand in the vicinity of the station. The best collecting place for the adult animals is at a depth of 10—20 meters outside the islet of Hållö. The young planktonic larvae were collected in an ordinary plankton net just outside the station. The older stages which were ready to metamorphose were better obtained in a type of plankton collector which caught the plankton organisms just over the bottom. These older larvae were reared and brought to the metamorphosis. In order to obtain lacking stages some of the young larvae were also reared. Newly metamorphosed larvae and juveniles were obtained in the same sand as the adult specimens.

The first larvae appeared in the plankton in the last week of July and then they were more or less regularly found to the end of August. During this time they never occurred in abundance and now and then they were completely absent for some days.

Most of the material was fixed in BOUIN's fluid. SMITH's and KLEINENBERG's mixtures for yolk-rich embryos were also used, but they did not give any advantages. The material was partly embedded and sectioned in paraffin after it had been oriented for sectioning in definite planes according to a recently described method (ÅKESSON 1961 a). Another part of the material was oriented and embedded in polyester wax. The sections were stained in azan, the iron haematoxylin of HEIDENHAIN, the haematoxylin of EHRLICH, the silver impregnation of BODIAN (ROMEIS 1948), in the chromic haematoxylin-phloxin of GOMORI (LILLIE 1948) and in the paraldehyde-fuchsin of GABE (1953). It should be mentioned that the silver impregnations were more successful in the polyester wax preparations than in the paraffin preparations.

The drawings of the larvae are based on photomicrographs of living larvae—in order to get a correct general habitus—and details from living and preserved material.

The drawings of sections are combined from several series, but always with the outlines from a camera lucida drawing of a single section.

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3. Morphology and Biology of the Larvae

a. PLANKTONIC LARVAE

The youngest larvae found in the plankton are metatrochophores with a length of about 200 μ. They have three pairs of parapodia rudiments. In living larvae the bristles rarely project from the tips of the parapodia which are flattened along the body, but in preserved specimens the bristles slightly project from the first and second pairs of parapodia. The bulky ventral part, posterior to the stomodaeum, projects caudally as a conical stylus with a length of 25—30 μ. This stylus bears the efferent opening of a prominent glandular organ, which causes the bulky appearance of the ventral part of the larvae (Fig. 2 A).

On the lateral parts of the episphere the larvae have a pair of pigment spots. In these young larvae they have a position on the ventral half of the episphere near the prototroch. There is no apical plate or apical tuft, the prospective cerebral ganglion is represented by two nuclei around and posterior to the eye spots.

Most of the episphere is occupied by the larval stomach. This is the most dominating part of the enteric cavity. The stomach is separated from the larval intestine by a transversal fold, which proceeds from the ventral wall of the enteric cavity. In this stage the proctodaeum is only indicated as a shallow pit without any communication with the intestinal cavity. The stomach and the intestine communicate by means of a narrow dorsal aperture.

The oesophagus forms a wide tube from the ciliated oral field to the stomach. The tube is slightly bent anteriad. The epithelium cells in the pointed angle between the oesophagus and the stomach are coloured by dark pigment granules. When the larvae are actively feeding in the culture bowls the oral field normally forms a wide funnel with a projecting upper lip.

The young metatrochophore described above agrees fairly well with the description and the rough sketch given by BANSE (1956 Fig. 2). With respect to the ciliation, however, his larvae are different. BANSE is of the opinion that the larvae described by GRAVELY (1909) as "Syllid A" are synonymous with the larvae of *Pisione remota*. As BANSE has access to only preserved material of the early larvae, he probably refers to GRAVELY when he states that the prototroch consists of two rows of cells, the anterior row bearing cilia with a length of 70 μ, the posterior one with cilia of 50 μ. In cross-sections of the prototroch of the youngest larvae the ciliation is uniform, but in older planktonic larvae with 5 pairs of setigerous parapodia or more the anterior row of thochoblasts are provided with two types of cilia as is seen in Fig. 5. The length of the cilia never exceeds 20 μ. A midventral tuft of cilia anterior to the prototroch is transitory and disappears in later larval stages when the lateral rudiments of the prospective cerebral ganglion fuse in the median plane.

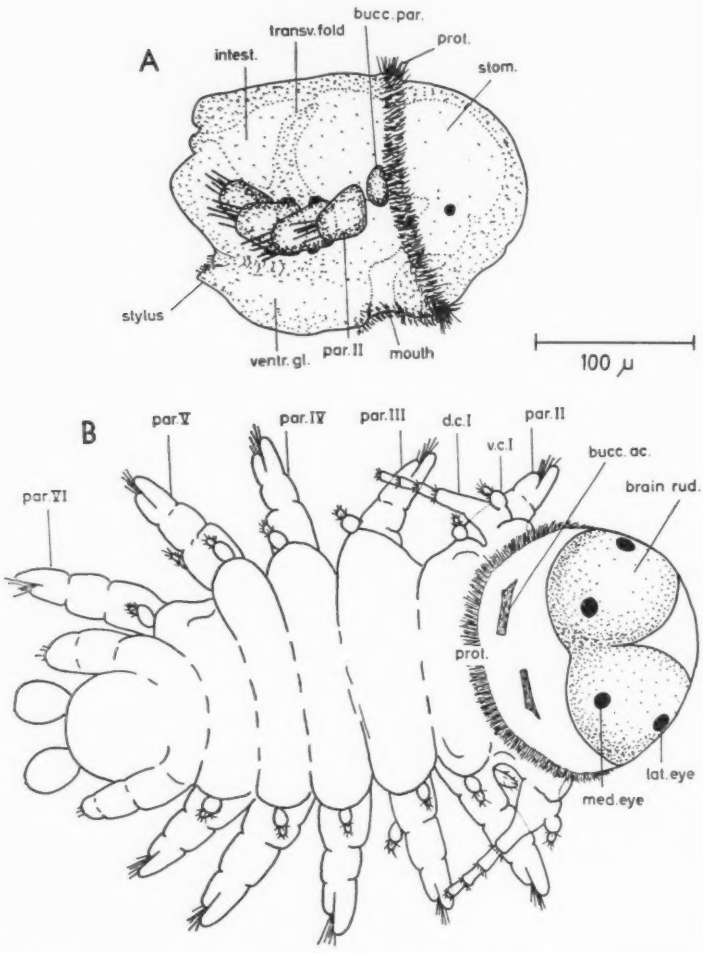

Fig. 2. Planktonic larvae of *Pisione remota*. Fig. A a young metatrochophora, Fig. B an older stage, not yet ready to metamorphose.

The larvae of the stage described above are good swimmers. Unlike older larvae they are easy to keep in culture bowls. They develop normally both in water from a depth of 30 meters with a salinity of 29 $^0/_{00}$ and in surface water with a salinity of 20 $^0/_{00}$. Except for the prominent stylus in the posterior ventral part the larvae are very similar to corresponding stages of polynoid larvae. AIYAR and ALIKUNHI (1940) report that the larvae of *Pisionidens indica* attach themselves to the bottom of the culture bowls by means of a secretion from the ventral gland and then execute quick rotatory movements. The larvae of *Pisione remota* also attach themselves to the bottom or to the surface-tension, but not

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by means of the secretion of the ventral gland. They use the secretion from a glandular area on the episphere just anterior to the prototroch.

When the larvae were kept in culture bowls they were fed with *Nitzschia closterium* and a small green flagellate, the name of which is unknown. When only small amounts from the food cultures were added to the bowls the true nature of the prominent ventral gland could be observed. The secretion from this gland formed a collecting apparatus, a slime net to which the food adhered. The posterior, or more correctly the dorsal, part of the stylus is provided with short cilia which form a continuation of a small ciliated field on the body. The conical slime net seems to be formed by the action of these cilia. The finer structures of the net were impossible to observe—as soon as the larvae were disturbed in any way they cast off the net.

Some of the young larvae just described were reared to the metamorphosis. Continuous series of larval stages were collected from the plankton and preserved for the histological study. A comparison showed that the reared larvae developed in a normal way. One of the oldest larvae normally found in the plankton is shown in Fig. 2 B. BANSE (l.c.) has depicted both younger and older stages. A second pair of eyes appear in larvae with 5—6 segments.

The growth of the planktonic stages includes an elongation of the trunk and a differentitation of the parapodia. New parapodia are successively added from the prepygidial growth-zone until the larvae have eight pairs. The third and subsequent pairs of parapodia develop globular dorsal and ventral cirri with terminal knobs. Like the appendages on the first and second segments the cirri are provided with palpocils. On the second segment, which is the first setigerous, the ventral cirri are subulate. On all setigerous segments the notopodium is only represented by the aciculum, which is much shorter than that of the setigerous neuropodial lobe. The number and arrangement of the setae agree with the description of the adults given by SOUTHERN (1914). There are four composite falcigerous setae around the neuropodial aciculum and a simple one in the dorsal part of the lobe. BANSE (l.c.) reports that sometimes the larvae have five composite setae, but in the present material the number is constantly four.

The most interesting development is seen in the parapodia of the buccal segment. The first traces of these appendages are seen when the larva already has four pairs of setigerous parapodia. In this segment the parapodial bases do not develop beyond the first rudiments, rounded knobs with a more dorsal position than the bases of the subsequent parapodia. From the posterior dorsal margins of these rudiments a pair of slender, tapering cirri develop. A second pair of cirri of the globular type grows out from the anterior ventral part of the rudimentary parapodial bases. Some hours after their first appearance they become attached to the bases of the slender cirri, which are now larger than the proper parapodia (Fig. 2 B). The bases of the buccal parapodia are now indicated only by the presence of the distal ends of a pair of large spines. These spines probably

represent the notopodial acicula of the buccal segment, which in the adult animals are found in the most anterior part of the head (Fig. 1).

The larvae feed actively during the whole planktonic stage. At the end of this period the cavities both of the stomach and of the intestine have more or less disappeared. This depends on an accumulation of food substance in the endoderm cells. Large globular vacuoles are seen in these cells (Figs. 5 and 7). As a result of the increased size of the intestinal cells the proctodaeum closes at the end of the pelagic stage. Somewhat later the stomodaeum is also closed when the pharynx is formed. Thus the larvae undergo the metamorphosis with both ends of the digestive tract closed.

b. METAMORPHOSING LARVAE

As already has been pointed out by BANSE (l.c.), the presence of a number of pisionid species on the beach of Madras (AIYAR and ALIKUNHI 1940) all of them on different types of sand bottoms indicates that the larvae have a power of rapid metamorphosis when they come into contact with the suitable substratum. It is a well-known fact that pelagic larvae are dependent on the bottom substratum and that they can postpone the metamorphosis if they do not come into contact with a suitable bottom substratum (THORSON 1946, WILSON 1952, HANNERZ 1956, ÅKESSON 1958). It may be questioned whether or not BANSE's oldest pelagic larvae have postponed the metamorphosis. They were collected on the beach of Kiel where the adult specimens are seldom found. They had 9 segments like the youngest ones from the sand. In the present material all the metamorphosing larvae have only 8 segments. But when the larvae were kept in bowls without any suitable substratum the pelagic period was prolonged for about ten days, after which the larvae died without any signs of a beginning metamorphosis. In most cases these larvae developed a ninth pair of parapodia and sometimes also the first rudiment of the tenth one.

A number of the oldest larvae collected from the plankton were reared in order to obtain the metamorphosing stages and the first bottom stages. Adult and juvenile specimens were collected from the sand which was brought to the laboratory from the natural habitat and placed in big aquaria with only little water over the sand. After one or two days the lack of oxygen had caused an accumulation of the animals in the surface layer of the sand.

When large planktonic larvae possessing eight segments were transferred to bowls with water taken from these aquaria and sometimes containing a little of the sand the metamorphosis normally began within two or three hours. The metamorphosis includes only the anterior end of the larva. No new segments are added during this time, even the youngest juveniles collected from the sand still have the same segment number as at the beginning of the metamorphosis.

The normal behavior of the larvae, when they have just been placed in the

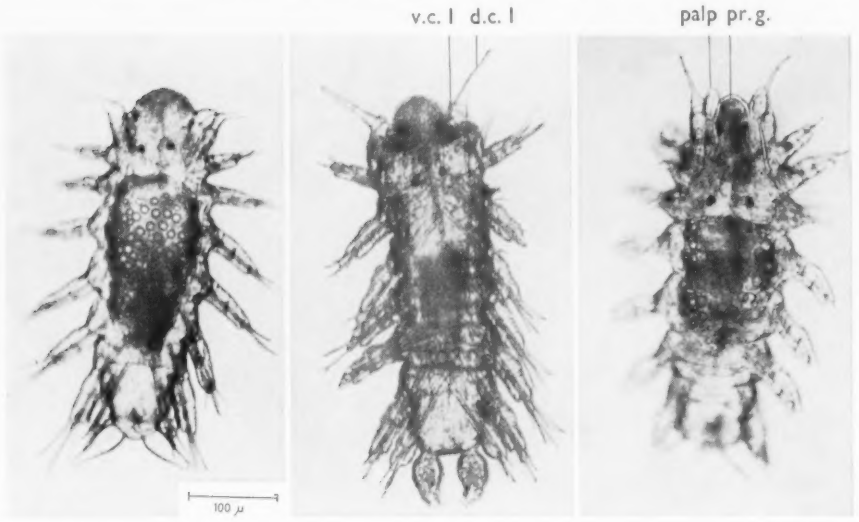

Fig. 3. Three larvae at different stages of metamorphosis. Photomicrograph of living larvae. Note the large vacuoles in the endoderm cells.

bowls, is to sink to the bottom and attach themselves to the glass or the sand grains by means of a secretion from the parapodial glands which have now begun to develop. Now and then during the first two hours they leave the bottom and swim around for a minute or more. They make no attempts to burrow down into the sand not even when the sand is sifted and only the smallest grains are used in the bowls. They lie more or less motionless on the surface of the substratum and can easily be mistaken for dying.

A closer examination of the larvae at intervals showed that the prototroch began to degenerate after about two hours. Six hours later all ciliary movements have disappeared. In the meanwhile the forward migration of the buccal appendages has begun. Simultaneously the brain migrates backwards and becomes compressed in the anterior part (Figs. 3 and 4). This rapid change of the position of the brain does not give the impression of being the result of cell divisions as much as the result of cell migrations. The best evidence of this interpretation is the change of the position and the form of the eyes. Especially the lateral eyes become elongated during the displacement towards the anterior end of the head.

As the stomodaeum is closed during the metamorphosis the larvae must resort to the stored food in the enteric epithelium. The amount of globular vacuoles is also successively diminished. But even juveniles from the sand which have added two new segments from the prepygidial growth-zone, still have some stored food in the endoderm cells. In more advanced larvae the pharynx has become protrusible and the enteric cavity contains food particles. These larvae dig actively through the substratum.

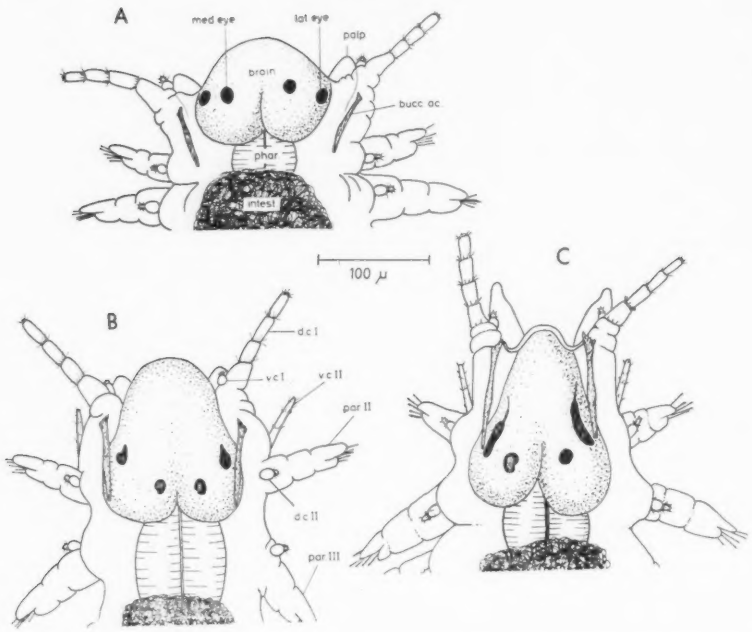

Fig. 4. Three larvae at different stages of metamorphosis. The buccal segment moves in an anterior direction (cf. Fig. 14).

From the end of the metamorphosis when the larvae have only eight segments they are perfect miniatures of the adults except that they have no genital organs and no traces of any segmental nephridia. In the adults nephridia occur in all setigerous segments except the three anterior ones. The gonads and the copulatory apparatus are found first in the eighteenth to twentieth segments and backwards.

4. Histogenesis

As the age of the larvae from the plankton samples is not known, it seems convenient to use the number of segments and other external morphological features as the basis of subdivision. In the following brief description of the different stages special attention has been paid to the organization of the head.

Planktonic stages

A. Larvae with 3 pairs of setigerous parapodia. The appendages of the buccal segment are not visible. 1 pair of eyes.

B. Larvae with 3—4 pairs of setigerous parapodia. The buccal appendages are visible as rounded protrusions. 1 pair of eyes.

C. Larvae with 6—7 segments. The dorsal cirri of the buccal segment are longer than the proper parapodia. Subulate ventral cirri have developed on the first setigerous segment. 2 pairs of eyes.

D. Larvae with 8 segments. The persisting prototroch is laterally somewhat displaced through the forward migration of the buccal parapodia. These larvae are ready for the metamorphosis.

Bottom stages

E. Larvae with 8 segments. The prototroch is vestigial or has disappeared. In a dorsal view the brain has a circular outline with the 4 eyes approximately at the same level (Fig. 4 A).

F. Larvae with 8 segments. One pair of eyes in the posterior part of the elongated brain, the other, the lateral pair, elongated (Fig. 4 B and C).

G. Larvae with 8 segments. The still more elongated brain extends to the posterior margin of the third setigerous segment. The two pairs of eyes are located in the anterior and posterior part of the brain respectively.

H. Larvae with 10 segments. The anterior end now has the adult organization. The anterior, originally lateral eye pair is more or less reduced.

As an introduction to the description of the histogenesis the histology of the smallest larvae collected from the plankton samples, the A-larvae, will be described. In the following part the different stages are referred to as the A-larvae, B-larvae, etc.

a. THE HISTOLOGY OF THE SMALLEST PLANKTONIC LARVAE

Ectodermal structures

The prototroch consists of two rows of trochoblasts which form a closed circlet around the larva. The ciliation is concentrated to a narrow band where most of the cilia are situated on the posterior trochoblast row (Fig. 5 A). The cilia have a length of 15—20 μ. Their roots can be traced back to the proximal part of the cells. A delicate circular nerve is seen between the two trochoblast rows. This nerve is followed on the inner side by a circular muscle, which in the ventral part is connected with the circular muscle around the stomodaeum. Like the prototroch muscle this is of an ectomesodermal origin.

The ectoderm of the episphere remains a single-layered epithelium except in its ventro-lateral parts immediately anterior to the prototroch where the two rudiments of the cerebral ganglion have developed by means of radial division. In

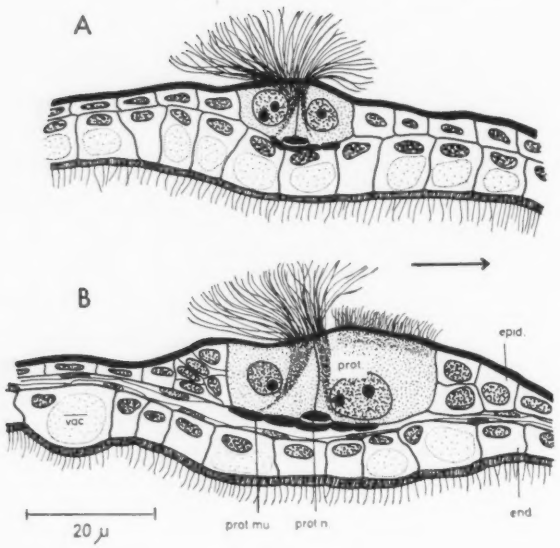

Fig. 5. Cross-sections through the prototroch. Fig. A a young metatrochophora, Fig. B a metatrochophora at the end of the pelagic stage. The arrow points in an anterior direction

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this early stage the two brain rudiments have a position in the main in the ventral half of the episphere (Fig. 6). Close to the prototroch they consist of several cell layers which are successively flattened out towards the margins. An ocellus is seen somewhat anterior to the centre of each brain rudiment. The ocelli have the form of pigment cups with the opening in a postero-lateral direction. As they have a diameter of only 7 μ their finer structures are beyond the limit of resolution of the light microscope, but the position of the surrounding cells makes it probable that the ocelli are of the inverted type.

The two rudiments of the cerebral ganglion are connected by a commissure which describes a curve at some distance from but approximately parallel to the prototroch. The lateral parts of this commissure are surrounded by neuroblasts, but the medial part is covered by undifferentiated flattened epidermal cells. Some of these epidermal cells just posterior to the commissure bear short cilia. Possibly this is a rudiment of the akrotroch.

Between the suggested akrotroch rudiment and the prototroch some of the epidermal cells have been enlarged and transformed into unicellular glands. These cylindrical gland cells have a length of 25—30 μ. Like the prototroch cells their nuclei are provided with large nucleoli. Two or three other gland cells are seen close to each ocellus (Fig. 7 A). The secretion of all these epispheral gland cells are PAS-positive. When stained in azan after a fixation in BOUIN's mixture the amorphous secretion has a basophilic reaction.

The lateral parts of the cerebral commissure continue backwards as the circumpharyngeal connectives. Immediately dorsal to the connectives each cerebral ganglion rudiment is connected to a demarcated cell group which forms an

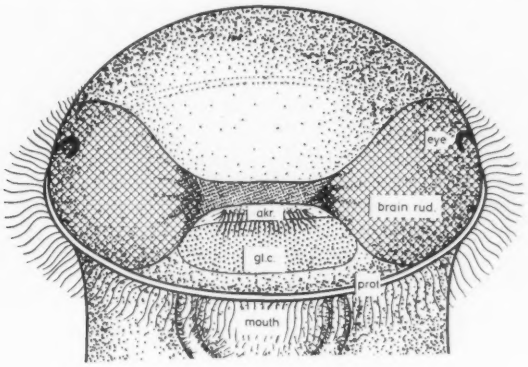

Fig. 6. A scheme of the early brain rudiments and adjacent structures. The connections with the hyposphere are not drawn.

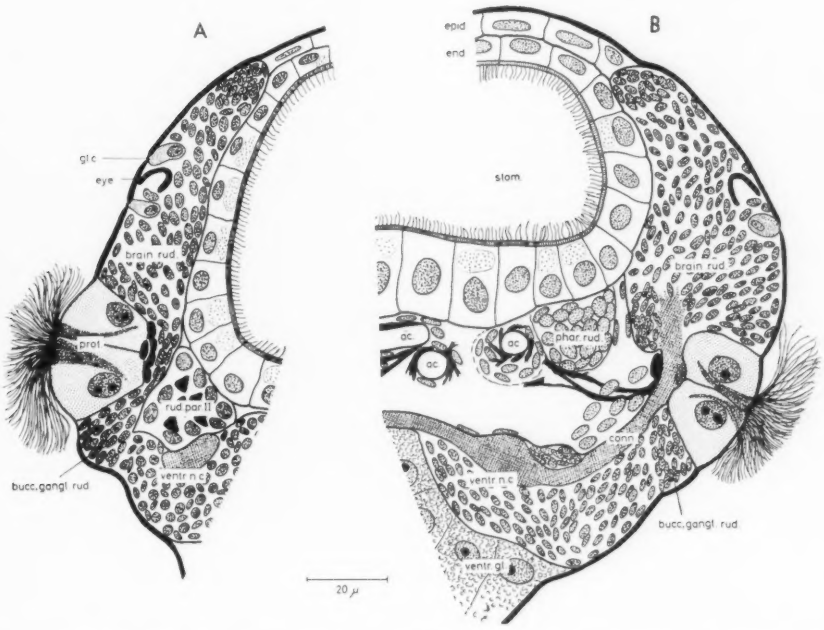

Fig. 7. The connections between the brain rudiment and the nerve cord. The sections are not in the same plane. Fig. A the cellular bridge posterior to the prototroch. In Fig. B is seen the dorsal root of the circumpharyngeal connective.

antero-dorsal continuation of the ventral nerve cord. Thus a cell bridge is established between the brain rudiment and the anterior part of the nerve cord. The cell bridge has the position as is seen in Fig. 7 A between the trochoblasts and the lateral parts of the nerve cord. In this early stage the cell group is not distincly demarcated from the nerve cord, but it is clearly demarcated from the

setal sacks. The proximal parts of the first pair of setal sacks project to the level of the prototroch.

The ventral nerve cord has not yet demarcated from the epidermal layer. Ventrally in the anterior part the two halves of the nerve cord are widely separated by the ventral gland, posterior to the gland they fuse mid-ventrally. They can be distinguished as two separate units except in the prepygidial growth zone where the neuroblasts form a crescentic region around the ventral and lateral parts of the proctodaeum.

The neuropile occupies a dorso-median position in each half of the nerve cord. In transversal sections its volume gradually becomes smaller towards the posterior part, and in the prepygidial growth zone the neuroblasts form an undifferentiated cell mass which has not developed any neuropile.

The neuropile proceeds in an antero-lateral direction as the circumpharyngeal connectives, which enter the two brain rudiments just ventral to the connexion between each rudiment and the lateral cell group mentioned above. The connectives pass lateral to the prototroch muscle, which here is slightly separated from the trochoblasts and connected to the circular muscle layer of the stomodaeum. At the level of the posterior margin of the prototroch region each connective branches into two nerves. One of these, the postero-lateral root, is seen in Fig. 7 B. The other has a more anterior position close to the enteric epithelium and forms a direct continuation of the cerebral commissure. The cells between the two roots form the prospective palp nucleus. It is obvious that the two roots are homologous with the dorsal and ventral branches of the adult circumpharyngeal connectives.

The prototroch nerve is connected to both branches of the circumpharyngeal connectives. It has not been possible to determine whether the neurones of this nerve are situated within the brain rudiments or in the ventral nerve cord, but the first-mentioned alternative seems to be probable.

The ventral gland forms a very prominent structure (Fig. 8). The gland cells are discoidal or slightly elliptical with the main axis directed towards the stylus in the ventral caudal part. The nuclei of the gland cells are situated along the dorsal and lateral margins. They have a diameter of about 8 μ. In each nucleus is found a large nucleolus. In the proximal part of the cells the secretion is distinctly granulated, more distally it has an amorphous structure and is partly removed during the preparation of the slides. Probably the granulae represent a pro-secretion. In azan both the granules and the secretion proper have a slight basophilic staining reaction. The cell boundaries are distinctly seen in the proximal part, but in the distal part they have disappeared thus forming a large central cavity midventrally anterior to the stylus.

The stylus has a length of 30—35 μ. In swimming larvae its main axis is parallel to the main axis of the body, in preserved larvae the stylus is often pointed more ventrally. The epidermal cells, which form a delicate sheath around the

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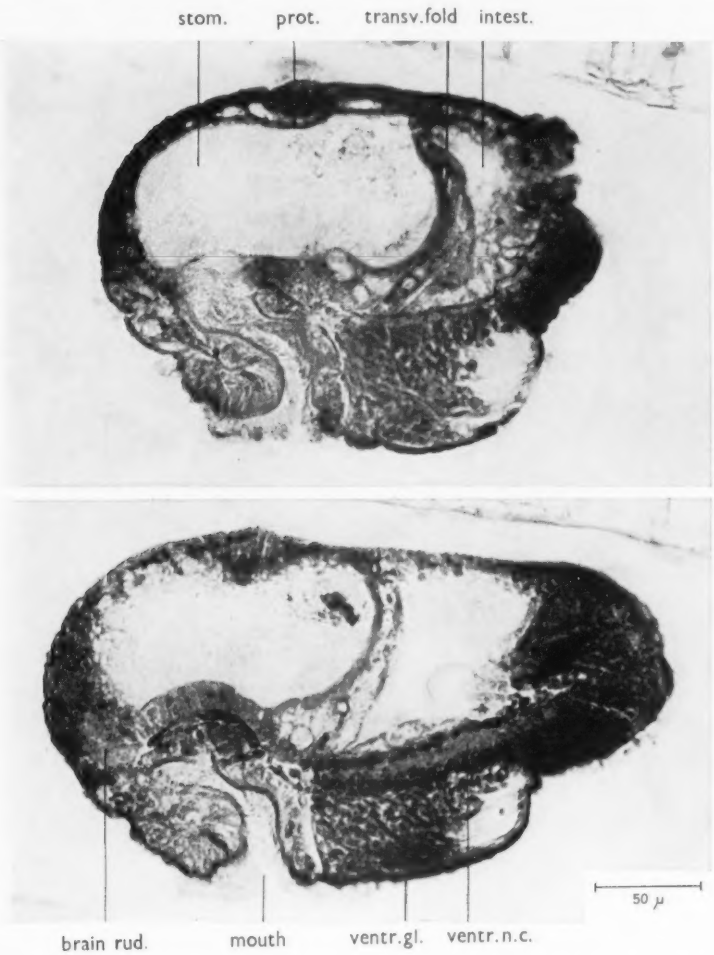

Fig. 8. Sagittal sections through 2 planktonic larvae. The sections have passed lateral to the stylus of the ventral gland. — Bouin, paraffin, 6 μ, A. HEIDENHAIN's iron haematox. — eosin; B. azan.

gland, are here somewhat higher, especially on the dorsal (caudal) surface of the stylus where they are provided with cilia. The slime net is formed from the secretion by the action of these cilia. The glandular duct forms a single aperture on the tip of the stylus. The opening is surrounded by a delicate sphincter muscle. *The parapodia* originate as lateral ingrowths of the ectoderm. In the youngest larvae only the three first pairs of setigerous parapodia project over the surface as conical, somewhat flattened elevations. In sections the subsequent parapodia buds are seen long before they project over the surface. When the setae appear

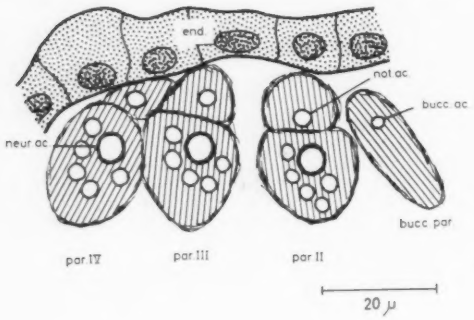

Fig. 9. A cross-section through the setal sacks of a young metatrochophora, drawn from a single section.

their first rudiments are visible at the same level in the bottom of the setal sacs but later the notopodial aciculum extends far longer towards the median plane.

In Fig. 9 the first four parapodia rudiments are seen in a transversal section. In the dorsal part of the first parapodium rudiment a single seta is visible. Later this seta develops into the stout aciculum of the buccal segment. Judging from the position and the later development of the seta it seems probable that it represents the notopodial aciculum.

In the second and subsequent parapodia the prominent neuropodial acicula are surrounded by five setae. Each notopodium is represented only by a demarcated cell mass around the single aciculum (Fig. 9).

The stomodaeum extends as a wide tube from the mouth in a dorsal and anterior direction. In the living larvae the mouth projects as a ciliated funnel just posterior to the prototroch. In the preserved larvae the middle and interior part of the lumen are somewhat flattened from the dorsal and ventral sides except in the passage to the stomach where it is depressed by the two lateral pharynx rudiments (Fig. 10). These consist in the youngest larvae of elongated cells which are radially arranged around small cavities.

The proctodaeum is represented by only a shallow pit, the inner part of which forms a narrow slit in the median plane. The ectoderm and the endoderm have not yet become confluent.

The larval nephridia could not be observed in the living larvae. They have a position inside the prototroch on the ventral side of the cell bridge mentioned above, between the brain rudiment and the lateral cell group just posterior to the prototroch. Between the cell bridge, the pharynx rudiment, and the proximal parts of the parapodia ingrowths the cavity is spacious. Each nephridium has the form of an irregular thin-walled sack which is composed of few cells. The sack is filled with globular granules which are slightly basophilic in azan. A delicate duct is visible extending to the surface just lateral to the anterior part of the nerve cord (Fig. 10).

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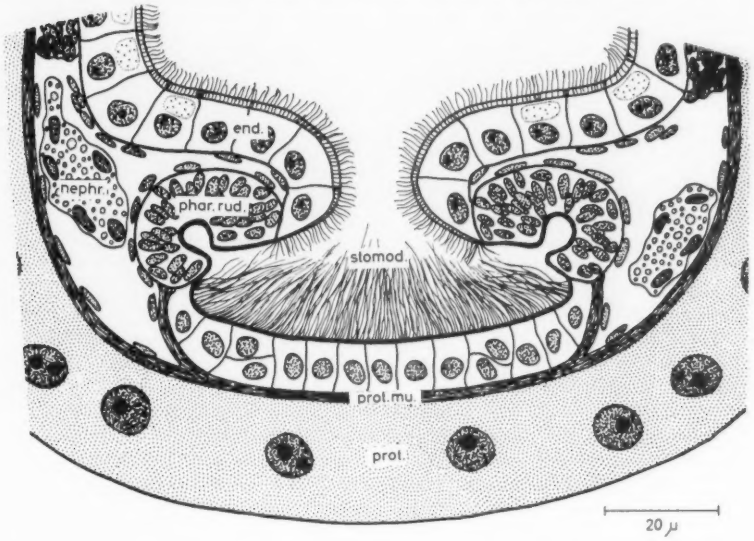

Fig. 10. A transversal section through the pharynx rudiments and the larval nephridia in a larva with 6 segments.

Endodermal structures

The stomodaeum opens into the endodermal stomach which forms the largest part of the enteric cavity (Fig. 8 A). The major part of the stomach is situated within the episphere. As the rudiments of the cerebral ganglion have not yet fused, the endoderm cells have a direct contact with the epidermal layer in the medial and dorsal parts of the episphere. The posterior part of the stomach is delimited from the larval intestine by a transversal fold, which extends from the ventral and lateral parts of the endoderm. A small dorso-median aperture forms the single communication between the two cavities. Food particles are visible in both cavities. It seems as if there is a certain accumulation of waste products in the intestine awaiting for the later formation of the anus.

The histological structure is the same in both regions. The endoderm cells have both a resorbing and a secretory function. They are provided with short cilia and a conspicuous striated border. Most cells contain large vacuoles with an amorphous content (Fig. 5, 7).

The cells of the ventral part of the stomach between the stomodaeum and the transversal fold are more than twice as high as other endoderm cells. They are wide transversely and flattened antero-posteriorly. Proximally the cells are filled with small dark pigment granules. In the posterior part of this region the cells become still higher and form the medial region of the transversal fold. This fold has obviously been formed in earlier stages of development as a double-walled

fold from the ventral and lateral parts of the enteric cavity. The nuclei of the two layers are situated in the periphery except around the dorsal aperture, which is lined with a number of small cells provided with long tufts of cilia.

Mesodermal structures

The available material of pisionid larvae does not form a suitable basis for a more detailed account of the origin of the mesodermal structures. In the youngest larvae the anterior ends of the mesordermal bands have already split in the normal schizocoelous fashion. Any arrangement in segmental coelomic sacs has not been observed. The spacious cavity around the stomodaeum and the proximal parts of the anterior setal sacks are lined with a delicate coelomic epithelium, but probably some of the cells in this region are of an ectomesenchymal origin. Posterior to this region the mesodermal bands appear as solid blocks without any traces of a metameric segmentation. They are situated close together between the nerve cord and the intestine. Longitudinal muscle bundles are visible between the mesodermal band and the nerve cord. These muscle bundles are more closely associated with the mesodermal bands than with the nerve cord, and judging from the conditions in other polychaetes they have differentiated from the mesoderm.

b. DIFFERENTIATION OF THE HEAD BEFORE THE METAMORPHOSIS

The brain

The volume of the two brain rudiments increases by continuous radial division. The neuroblasts spread successively over the episphere.

In the B-larvae the two cell groups have established contact in the ventral median plane. In the main the brain rudiment is still situated on the ventral half of the episphere. The unicellular glands are separated from the central commissure by a thin layer of nerve cells. Lateral to the gland cells the brain consists of several cell layers.

The central commissure of the brain is in close contact with the endodermal cells of the stomach. In the median part the commissure is divided into a dorsal and av ventral branch by delicate muscles which traverse from the stomach across the brain rudiment to the surface of the episphere. ANDERSON (1959) reports a similar condition in *Scoloplos armiger*. More laterally the commissure is undivided until it branches into the dorsal and ventral roots of the circumpharyngeal connectives. The two roots have the postero-lateral and antero-medial position which was described from the smallest larvae (p. 190).

The brain retains the cellular contact with the two cell groups posterior to the prototroch. The boundary between these cell groups and the anterior part of the nerve cord is now more clearly distinguishable than in the youngest larvae.

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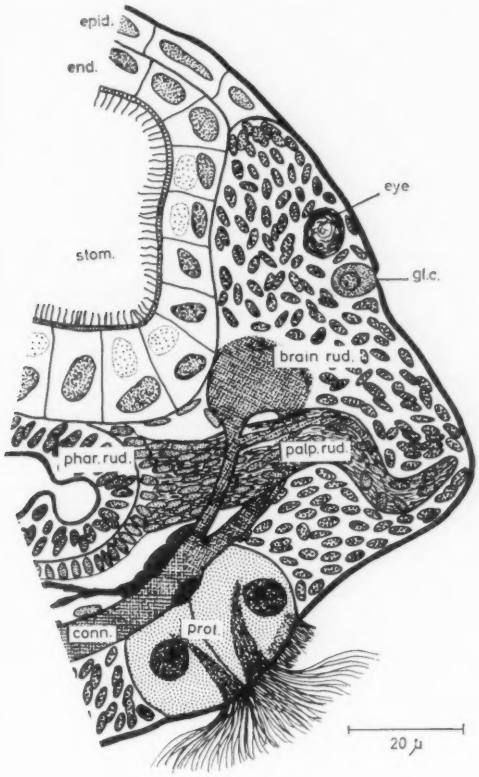

Fig. 11. The relation between the palp rudiment and the surrounding structures.

Formation of the palps

In the B-larvae and still more in the C-larvae the brain cells between the connective roots have been forced away by the mesodermal part of the earliest palp rudiment. The tip of the bud points towards the lateral surface of the brain slightly anterior to the prototroch. The cells of the mesodermal part are clearly demarcated from the surrounding brain cells. They are surrounded by a delicate connective tissue sheath (Figs. 11 and 12).

In *Harmothoe imbricata* and *Pholoe minuta* the first palp rudiments develop as in *Pisione*. KORN (1958) has described the palp rudiments in *H. imbricata*, but he has not observed the origin of the mesodermal part and the connective tissue sheath is erroneously described as as circularly arranged nerve net.

The dorsal root passes on the posterior side of the palp rudiment, the ventral one is closely connected to the base of the palp. The palp nerve is given off from the lateral side of the ventral circumpharyngeal root.

The palp muscles and other mesodermal components originate from the mesodermal lining of the spacious cavity around the stomodaeum. In the B-larvae

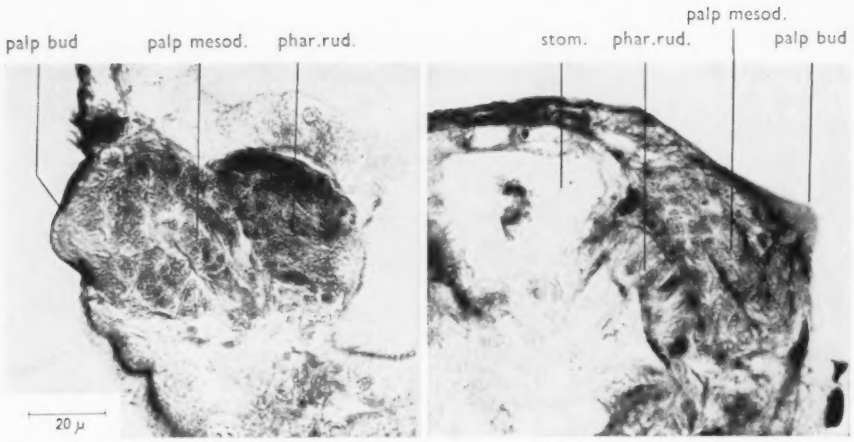

Fig. 12. Two sections through the S-shaped palp rudiments. The mesodermal central part is clearly demarcated from the surrounding brain cells. — Bouin, polyester wax, 6 μ, A azan, B paraldehyde fuchsin.

and the C-larvae these mesodermal cells are arranged as a sheath around each of the pharynx rudiments. From the antero-lateral part of this sheath a bridge of mesenchymal cells extends to the base of the palp rudiment. In the C-larvae the distal end of the cell cluster has differentiated into muscle cells.

In the D-larvae the prospective palps are visible as conical elevations on the ventro-lateral side of the episphere just anterior to the prototroch. In sections the central, mesodermal part has a characteristic S-form, which at the end of the pelagic stage is still more pronounced than the conditions seen in Fig. 12. The shape of the palp rudiments at this stage can possibly explain why the larvae at the beginning of the metamorphosis suddenly exhibit prominent palps which project from the ventral part of the head. This sudden appearance of the palps is true not only for the pisionid larvae but also for the aphroditid and nereid larvae. A comparison of the differentiation of the head in some of the errant polychaete families will be given in a later part of this paper.

Eye spots

A second pair of eye spots is first visible in the C-larvae. Often a new eye spot is only developed on one side. In the D-larvae, however, the second pair is always symmetrically developed. When the second pair of eye spots is first visible the ocelli are situated in the ventro-lateral parts of the two brain rudiments just anterior to the prospective palps. In the later part of the pelagic stage the fused brain rudiments successively move to a more dorsal position. This movement is synchronous with the differentiation of the first pair of parapodia. When the

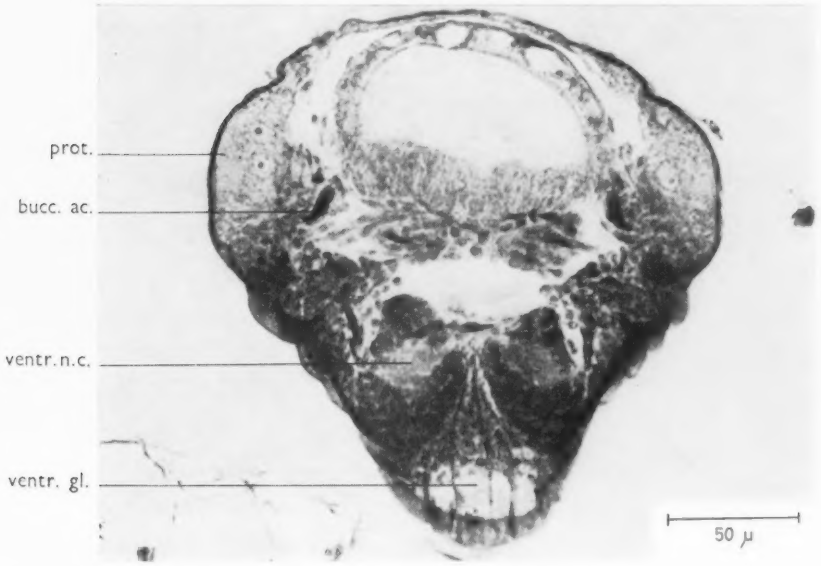

Fig. 13. Cross section through the first rudiments of the buccal acicula in a larva with 5 segments. Note the dorsal commissure between the two halves of the nerve cord. — Bouin, paraffin, 6 μ, azan.

larvae are ready to metamorphose and during the first hours of the metamorphosis, the two pairs of eye spots are visible at approximately the same level in a dorsal view (Fig. 4 A).

At the same time when the torsion of the brain rudiment becomes discernible the spacious cavity around the stomodaeum begins to extend into the episphere. Beginning in the posterior parts the future epidermal layer delaminates from the brain rudiment and the invading mesodermal elements differentiate into the muscles of the body-wall and into the brain capsule, a delicate sheath of connective tissue. The formation of this nonsegmental head-coelom is initiated mid-dorsally.

Buccal parapodia

An account of the differentiation of the head would not be complete without a description of the development and torsions of the first pair of parapodia. In the youngest larvae the formation of the acicula has just begun (Fig. 13). Very soon the acicula become very stout structures with a diameter of 5 μ, which is the size just posterior to the serrated tip. During the subsequent growth the diameter increases to about the double.

The parapodia of the buccal segment has a more dorsal position than those

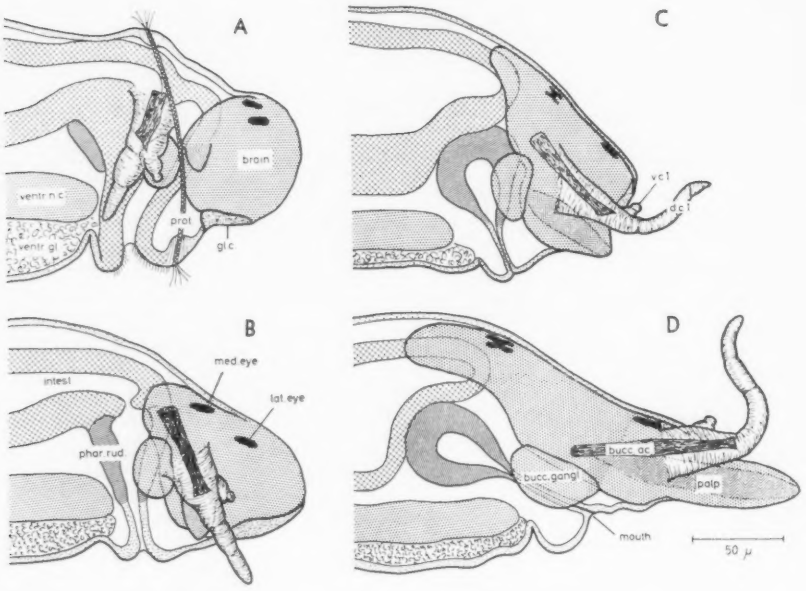

Fig. 14. A scheme of the head in lateral view showing the change in position of the buccal segment during the metamorphosis.

of the segments behind it. The acicula are directed in a posterior and slightly ventro-lateral direction when they first appear, but later their tips move in a dorsal and anterior direction until the acicula are situated horizontally in the transversal plane. The growth and torsion of the acicula occur at the same time as the differentiation of the parapodia, which has been described above. At the end of the pelagic stage the buccal parapodia are pointed in a lateral or antero-lateral direction. They are situated immediately posterior to the prototroch, which is partly displaced towards the apical pole.

c. CHANGES OF THE HEAD DURING THE METAMORPHOSIS

The rapid changes during the first hours of the metamorphosis is a result of cell migrations and torsions rather than of cell divisions. As a matter of fact mitoses are rare in the larvae of this stage except in the walls of the prospective pharynx and buccal cavity.

Before the trochoblasts have completely disintegrated, the torsions cause a displacement from the original position backwards in the dorsal part and in the opposite direction in the ventral part.

The torsion of the buccal parapodia continues in the way that is demonstrated in Fig. 14 until they have reached approximately the same position as in the adult animals at the end of the metamorphosis. The parapodia proper are vestigial and

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represented by only the projecting acicula. The ventral cirri retain the small and globular appearance, but they change from the original ventral position to the medial side of the bases of the prominent slender dorsal cirri.

Buccal ganglia

First now in the section series of the metamorphosing larvae is it possible to form an interpretation of the nature of the two lateral cell groups, which have a cellular connection with the cerebral ganglion (Fig. 15). These cell groups are the two separated halves of the ganglion of the buccal segment. Already in the A-larvae the halves are separated by the wide funnel-like mouth, and during the whole development they are as closely connected to the brain rudiment as to the ventral nerve cord. It is necessary, however, to observe that the cell groups are also connected to the anterior part of the circumpharyngeal connectives (Fig. 7). In the following part the two cell groups will be referred to as the buccal ganglia. At the same time when the buccal parapodia change their position also the buccal ganglia move in an antero-ventral direction and lose the cellular contact with the rest of the ventral nerve cord. At the end of the metamorphosis the ganglia have the same position as in the adults, i.e., antero-lateral to the connectives (Fig. 16).

The most important reason for considering the two ganglia as belonging to the buccal segment is the fact that in the adults as well as in the juveniles with 10 segments or more a delicate nerve can be traced from the buccal ganglion to a small podial ganglion at the base of the long dorsal cirrus. As could be expected from the displacement of the buccal parapodia, these nerves pass on the lateral side of the palps (Fig. 17).

The possibility that these ganglia are nothing but podial ganglia of the buccal segment and that the structure described above as the podial ganglion is a cirrus ganglion must also be taken into consideration. There are, however, some facts speaking against such an interpretation: 1. No cirrus ganglia have been observed in the setigerous segments of the adults (Fig. 12), 2. The first rudiments are visible as prominent structures in cellular contact with both the brain rudiment and the nerve cord when the buccal appendages still have the form of small and undifferentiated buds.

It is easily demonstrated that the close connection between the brain and the buccal ganglia is retained also in the adults. In Fig. 17 A the circumpharyngeal connectives are compressed, in Fig. 14 B where the pharynx is protruded, they are extended. The ganglia have the same position in close contact with the ventro-lateral surface of the brain.

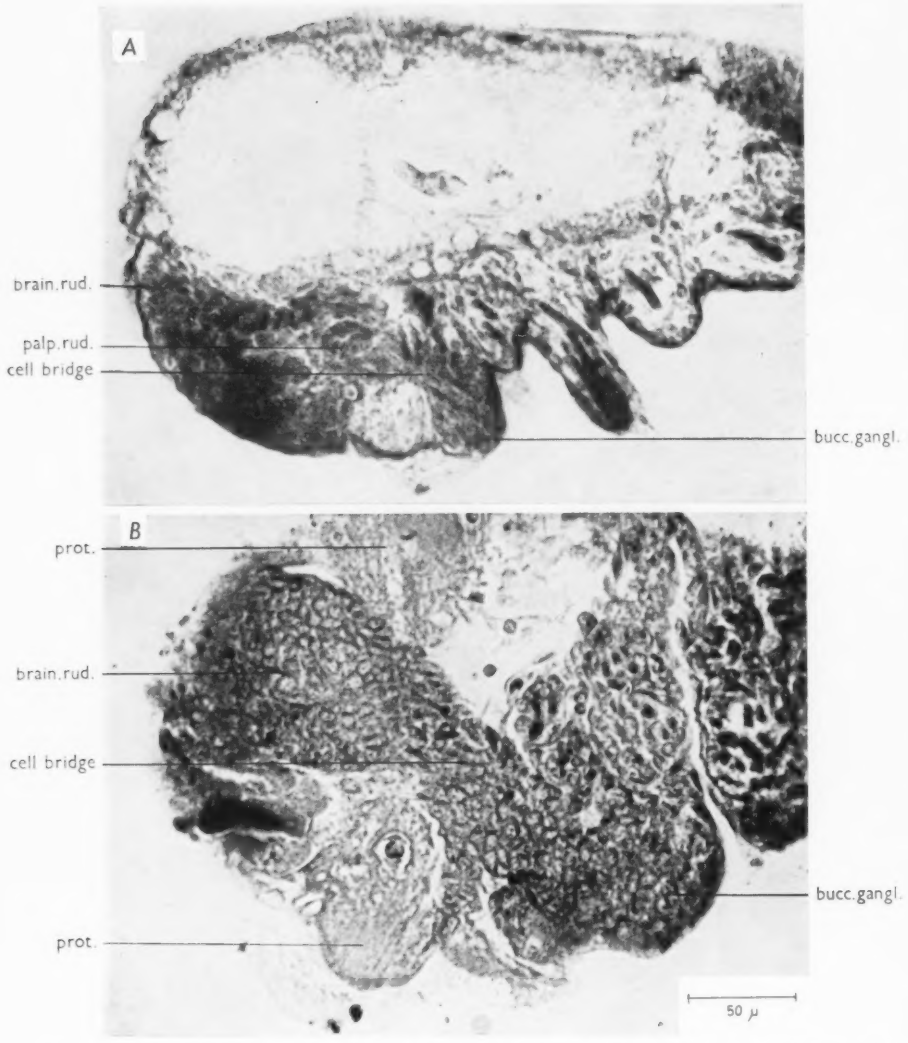

Fig. 15. Tangential sections through the cellular bridge between the brain rudiment and the ventral nerve cord. Fig. A *Pisione remota*, metatrochophore, Fig. B the same stage of *Harmothoe imbricata*. — Bouin, paraffin, 6 μ, azan.

Palps

The palps develop during the metamorphosis from the small conical rudiments to stout projections. At the end of the metamorphosis they are of the same length as the long cirri of the first segment. The torsion of the palps is similar to that

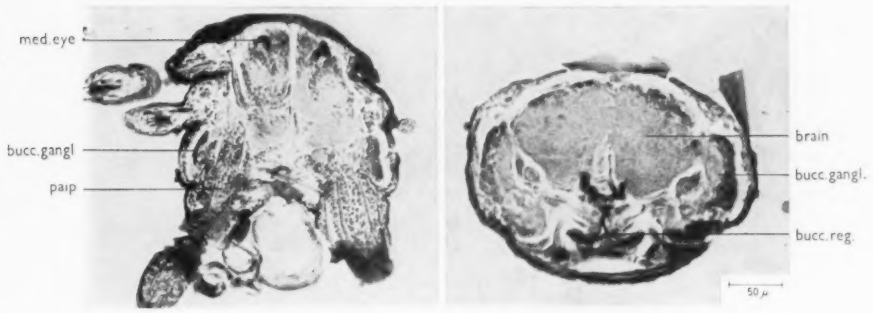

Fig. 16. Cross-sections through the brain and buccal ganglia in adult specimens of *Pisione remota*. — Bouin, paraffin, 6 μ, azan.

of the buccal appendages. At the end of the metamorphosis the palps are situated ventro-lateral to the buccal cirri (Fig. 14).

Differentiation of the brain.

In the last pelagic stages the brain rudiment had begun to separate from the epidermal layer, and at the same time mesoblasts invade the interspace. This process proceeds during the metamorphosis and is a condition precedent to the changes in shape and position of the brain. At the end of the period the posterior part forms two prominent lobes which extend to the level of the third setigerous segment. In the caudal part of these lobes the neurones are poor in cytoplasm and stain intensely in most nuclear stains. This is the first rudiment of the globuli of the corpora pedunculata. Their stalks do not form any discernible structures in juveniles with less than 10 segments.

When the separation of the brain from the overlying epidermis is completed, the eye spots have acquired a superficial position on the dorsal surface of the brain. The changes in the shape and position of the eye spots will give a good apprehension of the cell migrations and torsions. In the beginning of the metamorphosis the two pairs of eyes have a rounded shape, the medial pair is somewhat anterior to the lateral one. Later the medial eyes assume a more caudal position with the rounded shape retained, while on the other hand the lateral pair elongate and move in an anterior direction (Fig. 3 and 4). When this movement begins, the anterior end of the eyes assumes the shape of a thin pigmented cord, in the later stage of the movement the caudal part of the eyes has the same shape. Obviously the pigmented cells are detached from the surrounding tissues and migrate toward the anterior end. Here they are never organized as eyes, they have the shape of diffuse pigmented patches which are successively resorbed.

At the end of the metamorphosis the medial pair of eye spots has differentiated

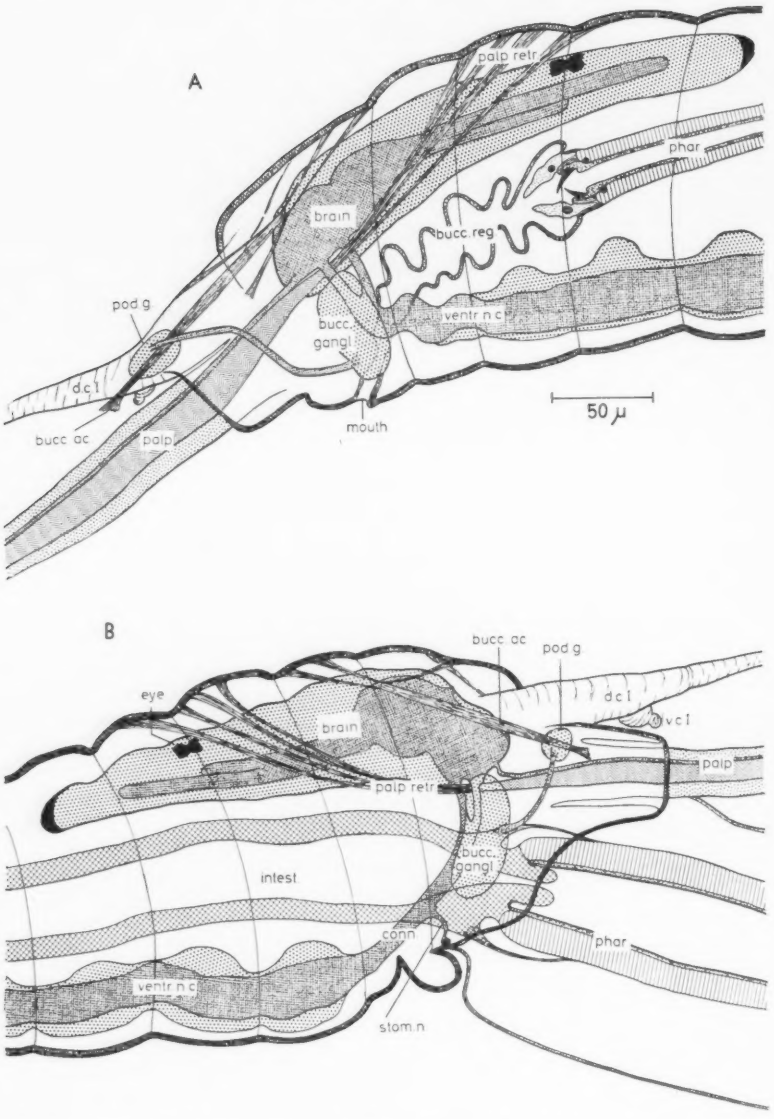

Fig. 17. The head of *Pisione remota*. In Fig. A the proboscis is withdrawn, in Fig. B it is protruded. In both cases the buccal ganglion has the same position close to the brain.

into two double inverted eyes. In juveniles with 10 segments or more another pigmented area arises as a semispherical cup around the most caudal part of each brain lobe. However, there is no evidence supporting an assumption that these pigment cups are photo-receptive structures.

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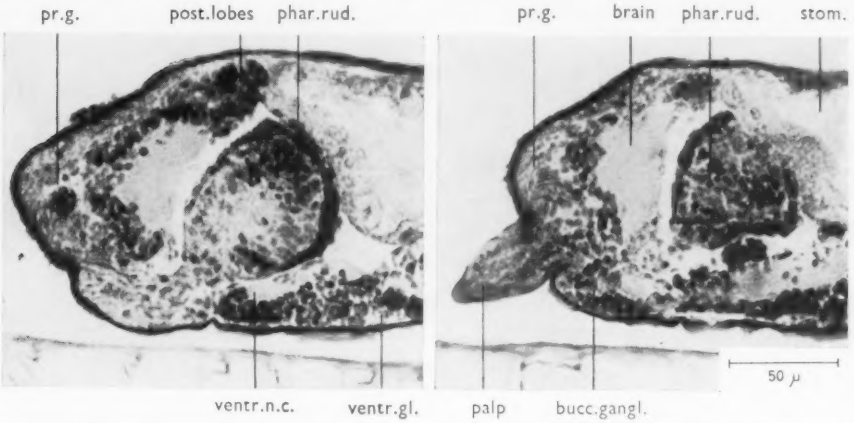

Fig. 18. Two consecutive sections through the head of a larva at the end of the metamorphosis. The buccal ganglia are now found ventro-lateral to the brain. The disintegrated gland cells are visible in the "prostomial ganglion". — Bouin, paraffin, 6 μ, azan.

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Glandular structures

During the pelagic stages the secretion from the mid-ventral glandular area of the episphere is given off on the surface through narrow apertures. When the epidermal layer is established in this region the gland cells lose their ducts, sink down from the surface and begin to degenerate. By torsions these degenerating gland cells move towards the most anterior tip of the prostomium where they are visible between the not yet fused bases of the buccal parapodia (Fig. 18). Later this area develops into the characteristic triangular structure which is visible in the adults posterior to the fused bases of the buccal parapodia (Fig. 1). The structure becomes successively separated from the brain proper by the fibrous brain capsule. SIEWING (1952) describes it as the "prostomial ganglion" in *Pizione remota* and *P. puzae* and pictures two delicate nerves originating from the central neuropile of the brain. He mentions the possibility that this postulated ganglion is the rudiment of the hind brain. In the present material, however, it has not been possible to trace any nerves connecting this structure with the brain neuropile and in juvenile specimens the cells still have the appearance of degenerating gland cells and not of neurones. But in the adults some dorsal cells in the mid brain region can form a separate nucleus which is partly situated within an interruption in the brain capsule. Possibly this is the last rudiment of an unpaired median antenna. In *Pisionella hancocki,* the only member of the genus *Pisionella* created by HARTMAN (1941), the prostomium has a conspicuous median antenna just at the place where the members of the genus *Pisione* have the "prostomial ganglion".

Also the glandular cells, which in the pelagic larvae are found close to the

eye spots, contribute to the structures of the adult brain. In the ventral part of the posterior lobes just anterior to the densely aggregated globuli cells of the corpora pedunculata the descendants of these cells are found. The close connection with the eyes is retained. The gland cells occupy the ventro-lateral part of the lobes, the eyes are situated in the dorsal or dorso-lateral part. Even if these gland cells are situated within the brain capsule, they must be interpreted as incorporated epidermal gland cells and not as neurosecretory cells. The definition of a neurosecretory cell and the possible origin of neurosecretory cells will be discussed in a later part of this paper.

d. THE DIFFERENTIATION OF THE VENTRAL NERVE CORD AND THE VENTRAL GLAND

Nerve cord

Similar to the cerebral ganglion the ventral nerve cord also becomes successively demarcated from the overlying epidermal layer and the interspace is invaded by mesodermal cells. The segmental arrangement of the ganglia is indistinct not only in the larvae but also in the adults. In the larvae the commissures are easily seen in the anterior part of the nerve cord where the two lateral halves are widely separated by the ventral gland. Even in juvenile and adult specimens where the gland has completely disappeared the lateral halves are more distinctly separated than in the posterior parts of the nerve cord. This seems to be a matter of common occurrence in the pisionids. AIYAR and ALIKUNHI (1940) describe the different degree of fusing in different regions of *Pisionidens indica*. They also give a rough sketch of the early trochophore which is provided with a ventral stylus indicating the presence of a ventral gland as in the larvae of *Pisione remota*.

The segmental commissures connect the dorsal parts of the ganglia in the pelagic and metamorphosing larvae. This is easily visible in the region where the two cords are separated. More posteriorly, in adult animals also in the anterior part of the nerve cord, the commissures connect the ventral parts of the diffuse ganglia. Obviously this is the result of a torsion in connection with the disappearance of the gland cells.

In the middle of each segment a podial ganglion is situated at the ventral base of the parapodium. In adult animals the connection with the nerve cord is easily demonstrated (Fig. 19) and in good silver impregnations centripetal fibers from the neurosensory cells of the cirri can be traced back to the podial ganglion. The podial nerves are visible only in the D-larvae and later stages. The podial ganglia, however, are visible already in the B-larvae. They are especially prominent in the second segment, which later develops the long, subulate ventral cirri.

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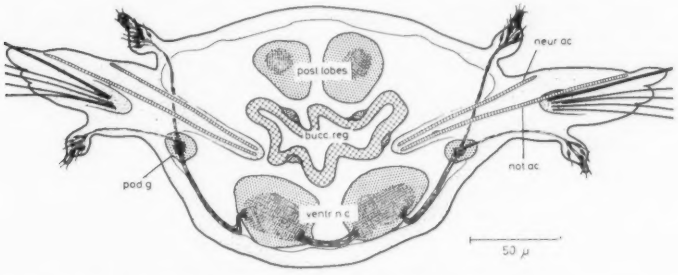

Fig. 19. A cross section through the third segment in a post-metamorphosed larva with 14 segments. The ventral gland is now disintegrated and the commissure has changed to a ventral position (cf. Fig. 13).

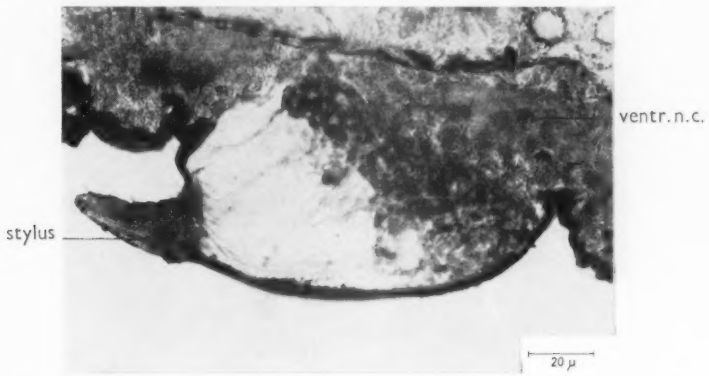

Fig. 20. Ventral gland with stylus from a planktonic larva with 6 segments. The nuclei of the gland cells are not visible. — Bouin, polyester wax, 6 μ, Bodian.

Ventral gland

The structure and arrangement of the cells in the ventral gland have already been described from the A-larvae and are also seen in Fig. 20. No histological differences are visible in the B- and C-larvae. The gland becomes successively elongated until it reaches the maximum size with a length of 150 μ.

In the D-larvae, i.e., at the end of the pelagic stage, the first signs of a disintegration are visible. They are manifested as a dissolution of the distinct boundaries between the gland and the nerve cord as also in the formation of intensely stained bodies of irregular size (Fig. 21).

The disintegration of the gland proceeds during the metamorphosis, which seems to be as much a period of strong torsions and cell migrations in this region as in the brain region. The gland is successively replaced from the ventro-lateral parts of the body wall. The strong longitudinal muscle bundles, which originally are visible on the dorsal surface of the nerve cord assume a ventro-lateral posi-

Fig. 21. Sagittal section through 2 metamorphosing larvae. Fig. A in the middle, Fig. B at the end of the metamorphosis. Note the detachment of the brain and the disintegrating prototroch. — Bouin, paraffin, 6 μ, azan.

tion. The main part of the deeply stained secretion bodies seems to be forced into the coelomic cavity, but some of them can also be found within the nerve cord completely surrounded by the neurones. Often the large, easily recognizable nuclei are also seen within or at the margin of the nerve cord. It has not been possible, however, to determine whether they become disintegrated or if they change their properties and are incorporated into the nerve chain. Nor is it possible to demonstrate any neurosecretory or other glandular structures within the ventral nerve cord of the adult animals.

e. THE PARAPODIA

Like most small animals living in the interstices of sandy bottoms *Pisione remota* is provided with adhering glands. In the adults prominent glands open on the dorsal lappet of each parapodium and on the medial side of the ventral cirrus. The dorsal gland is the more prominent. It consists of a number of gland

cells which are situated in the middle dorsal part of the parapodium. Each cell has a separate duct which opens on the distal part of the dorsal lappet. The secretion is intensely stained in the stainings according to GABE and GOMORI.

When the secretory activity of the gland cells first begins in the oldest planktonic larvae, the gland cells are situated within the epidermal layer and obviously they are derived from the epidermis.

In the parapodia of the buccal segment there is another type of secretory epidermal cells. When the stout acicula have reached the surface of the parapodia rudiment their tips are surrounded by distinct sheaths, all the cells of which are secretetory. The surface layer of the acicula is probably formed from these cells.

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f. THE DIGESTIVE TRACT

Formation of the pharynx

In the youngest larvae the first rudiment of the pharynx has already begun to differentiate. Laterally at the inner end of the stomodaeum the paired pharynx rudiment is seen as two crescentic evaginations from the stomodaeum wall (Fig. 10). Originally each of these consists of a single layer of elongated cells. The surface towards the small cavity is lined with a cuticula. Also peripherally there is a well-demarcated surface towards the blastocoele. The latter cavity, however, is soon invaded by mesoblasts, the origin of which is unknown. Probably they are ectomesoblasts (HÄCKER 1895), but is is also possible that they are derived from the anterior end of the mesodermal bands. Some of these mesoblasts arrange themselves in a thin sheath around the pharynx rudiments. Between the two structures a delicate layer of connective tissue is formed. At the same time the cells of the single layer of the pharynx rudiments divide into the clusters seen in Fig. 10. In later stages, in C- and D-larvae, the mesoblast sheath becomes a prominent structure, even if it still consists of a single cell layer. First the cells cover the two pharynx rudiments, later the two groups establish a contact with each other in the narrow interspace between the stomodaeum and the stomach. In a much later stage this external sheath differentiates into the heavy radiating muscle layer of the pharynx.

The formation of the pharynx rudiment is rather similar in all studied polychaete groups, but the apprehension of the origin of the different layers seems to be controversial. Recently KORN (1958) described the formation in *Harmothoe imbricata* and *H. sarsi*. KORN has accepted KLEINENBERG's (1886) and HÄCKER's (1895) opinion that the peripheral layer originates through a delamination from the first pharynx rudiment. This statement was rejected already by MEYER (1901) in favour of the disreputable theory of the "Neuromuskelanlagen". In addition to the continuous larval stages of *Pisione remota,* where the pharynx rudiments of the youngest larvae have the simple structure described above, the present

writer has also access to large series of larvae belonging to the families Nereidae, Aphroditidae, Phyllodocidae and others. This material has not yet undergone a more detailed examination, but with regard to the formation of the pharynx there are no facts contradicting the statement that the radiating muscle layer is derived from mesoblasts. It is a notable fact that also KORN describes the presence of mesoblasts between the stomodaeum and the stomach in stages where the pharynx rudiment still consists of a single cell layer.

In the G-larvae, at the end of the metamorphosis, the prospective radiating muscle layer is still organized as a single layer of elongated radiating cells without any traces of muscle fibers. In the juveniles with 10 segments or more from the sand the radiating muscle layer has differentiated and the pharynx is functional.

Only the inner part of the stomodaeum differentiates into the pharynx. The outer part gives origin to the thin-walled buccal region, i.e., that part of the stomodaeum which covers the protruded pharynx. The cavity is lined with a cuticula. Some of the cells differentiate into unicellular glands. At the boundary between the buccal cavity and the pharynx the epidermis forms a number of conical papillae which form a circlet on the protruded pharynx just anterior to the chitinous teeth. The latter are visible as one pair in the dorsal and one in the ventral pharynx wall. They are not visible in the oldest reared larvae but are present in the smallest juveniles, which were collected in the sand, thus it is obvious that here we have a gap in the series.

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The stomatogastric nervous system

In the description of the nervous system the stomatogastric system was not mentioned. A small nerve is given off from each circumpharyngeal connective caudal to the buccal ganglion. It is very interesting indeed that the stomatogastric nerves are given off caudal to the connection between the buccal ganglion and the connective. Unfortunately it has not been possible to observe the delicate nerves from their first appearance. They are only visible in sections of juvenile specimens from the sand and in the adults. Nor is it possible to trace the nerves within the connectives. The present writer is inclined to regard the peculiar origin of the stomatogastric nerves as a result of the special modifications in the head of the pisionids. The great variability with respect to the origin of the stomatogastric nerves in polychaetes has recently been pointed out by VON HAFFNER (1959), who is of the opinion that unlike the more highly organized arthropods the origin of the stomatogastric nerves in polychaetes has not yet been established.

The two stomatogastric nerves reach the mouth laterally. They give rise to the nerve net of the intestine. Both in the wall of the buccal region and in the pharynx there are four main nerves, two dorso-laterally and two ventro-laterally. In the anterior end of the pharynx they are connected by a ring nerve at the

Fig. 22. Anterior end of the protruded pharynx from a juvenile *Pisione remota* with 20 segments. — Bouin, polyester wax, 6 μ, azan.

base of the small papilla (Fig. 22). Neurones surround the connections and form four small ganglia.

The endoderm

The separation of the enteric cavity into the stomach and the intestine persists during the larval development. The proctodaeal opening is established in the C-larvae but is closed again at the end of the pelagic stage. This closure depends on an accumulation of reserve food in the endoderm cells which proceeds during the whole planktonic life. The accumulation begins in the ventral cells of the intestine and is later especially discernible in the ventral stomach cells just anterior to the transversal fold. The cells retain the structure with short cilia and large vacuoles which was described in the youngest larvae, but the whole cells become successively enlarged. As a result of this accumulation of reserve food the cavity of the intestine is almost obliterated and also the stomach cavity is considerably diminished. This is best seen in the oldest planktonic larvae and in those which have just begun the metamorphosis.

The closure of the stomodaeum at the beginning of the metamorphosis seems to be a condition precedent to the far-reaching torsions and cell migrations in the anterior region. By the action of the prominent circular muscle layer of the stomodaeum, which is already present in young larvae the wide funnel-like external part is completely closed. This will mean that the larvae are restricted to the reserve of the endoderm cells during the whole metamorphosis and also during the first time afterwards. The size of the endoderm cells and the enclosed vacuoles is successively decreased and the obliterated intestinal cavity appears again. The prominent transversal fold between the larval stomach and the intestine must be considered as a typical larval structure. It does not disappear during the metamorphosis but can still be traced in juveniles with 10—14 segments.

5. THE POSSIBLE AFFINITIES OF THE FAMILY PISIONIDAE

As an introduction to a discussion of the affinities of the pisionids it seems convenient to begin with a summing up of the most characteristic features in the larval and later development. Such features, which are common to all errant polychaete larvae or are subject of great variation even within distinct groups, have been omitted.

1. The cerebral ganglion originates from two ventro-lateral rudiments just anterior to the prototroch. There is no apical brain rudiment.

2. The brain separates from the ectoderm and extends as two posterior lobes to the level of the fifth segment. The corpora pedunculata occupy the posterior part of these lobes.

3. There are two pairs of larval ocelli, one of which develops into the adult eyes.

4. Numerous gland cells are found in the episphere. Some of them are later incorporated into the brain.

5. The two halves of the buccal ganglion are closely associated with the brain. The connection is seen in early stages as a cell bridge posterior to the prototroch.

6. The reduced buccal parapodia form the anterior end of the animal.

7. The larvae feed on nannoplankton which is caught by a slime net produced by the action of a prominent ventral gland.

8. The larval intestine is separated into a large stomach and a small intestine by a transversal fold. Reserve food is accumulated in the endoderm cells before the metamorphosis.

9. The pharynx is armed with two pairs of chitinous jaws, and anterior to these there is a circlet of terminal papillae.

The following comparisons with other families are largely based on the writer's own material. The study of this material is still in progress, so the observations mentioned here must be considered as preliminary notes.

a. COMPARISON WITH THE FAMILY APHRODITIDAE

In agreement with Banse (1956) it must be pointed out that the pisionid larvae are of the same general type as those found in the aphroditid genera *Harmothoe, Pholoe* and others. With exception of the presence of the ventral gland and its stylus in the pelagic stages of the pisionid larvae they have exactly the same habitus as young aphroditid larvae before the elythra have developed.

In the *Polynoe*-larvae (Häcker 1895) and the *Harmothoe*-larvae (Korn 1958) the brain originates from two lateral rudiments and a median one which represents the first bud of the median antenna. No such antenna is present in *Pisione remota.*

In most aphroditids the brain retains a close connection with the epidermis, but in *Pholoe* (sub-family Sigalioninae) we find exactly the same conditions as

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in *Pisione*. Two lobes extend backwards and contain the corpora pedunculata. The median antenna in *Pholoe* has no counterpart in larvae or adults of *Pisione remota,* but in *Pisionella hancocki* there is a median antenna with the same position as in *Pholoe*.

Most described aphroditid larvae have two or three pairs of larval ocelli, the fate of which is not known.

In respect to the gland cells of the episphere there is a striking resemblance even in details between *Pisione remota* and the aphroditids. Larvae of *Harmothoe* and *Pholoe* have a large glandular area on the ventral half of the episphere, where also some rudiments of an akrotroch is visible. Other gland cells are closely connected to the eye spots. KORN (l.c.) has given a detailed description of the incorporation of gland cells into the cerebral ganglion.

The close association between the brain and the buccal ganglion is a recent confirmation of HÄCKER's statement that in the young *Polynoe*-larvae the lateral brain rudiments and the anterior parts of the ventral nerve cord rudiment have a cellular connection. "Es sei hier nur erwähnt, dass in den jüngsten mir vorliegenden Stadien die beiden kleinzelligen Ectodermverdickungen, welche die Anlagen des obern Schlundganglions darstellen (Fig. 10 u. 11 osg), sich in continuirlichem Zusammenhang mit den Anlagen des Bauchmarks befunden." (l.c. pp 258—59). KORN has not observed this connection in *Harmothoe imbricata* and *H. sarsi,* but the present writer has found exactly the same connections as in *Pisione remota* in his material of *H. imbricata* and *Pholoe minuta* (Fig. 15). In juvenile specimens of *Leanira tetragona* with a total length of 0.8 mm, where the first few segments point in an anterior direction the buccal ganglion has a position very similar to that in *Pisione remota.*

With respect to the buccal parapodia there is a great range of variation within the aphroditids. Normally they point in an anterior direction, but the presence or absence of seta and the number of acicula is different even within the genera.

The extreme development of a ventral gland in close connection with the nerve cord has no counterpart in the studied aphroditid larvae. However, HÄCKER (1897) described a ventral stylus in a *Polynoe* sp. from Naples, although the possibility cannot be excluded that he described a pisionid larva. Both in larvae of the *Harmothoe* species and in *Pholoe*-larvae there is a small gland midventrally in the posterior part of the trochophore and metatrochophore stages (Fig. 23).

Judging from discriptions (RASMUSSEN 1956, KORN 1958) and from the writer's own experience all aphroditid larvae have the intestine separated into two parts by a transversal fold. Reserve food is accumulated during the pelagic stage especially in the cells of the intestine and those of the transversal fold, but not to the same extreme extent as in the larvae of *Pisione remota.*

According to HARTMAN (1941) the proboscis of the pisionids is of the scaleworm type. The two pairs of chitinuous jaws and the terminal crown of papillae are common to all aphroditid polychaetes.

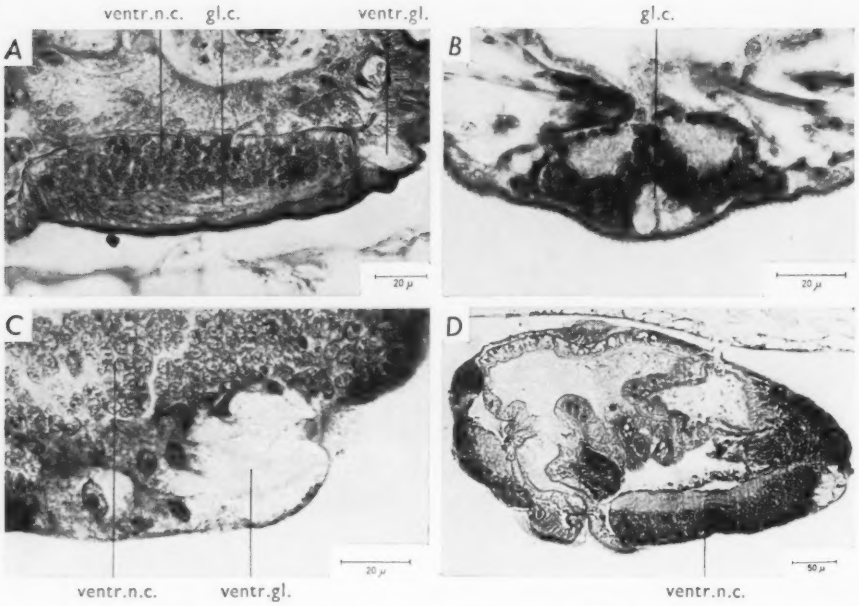

Fig. 23. Three median sections, A, C, D, and one cross-section, B, through the ventral nerve cord and the ventral gland. Fig. A and B are from metatrochophores of *Pholoe minuta*, Fig. C and D from Harmothoe imbricata. The anterior gland cells in *Pholoe minuta* are very transitory structures. — Bouin, paraffin, 6 μ, azan.

In order to counterbalance the exceptionally good resemblances between the families Pisionidae and Aphroditidae, which have been evident from the comparison above, we must search for any fundamental differences between them. Three such differences are of special interest: 1. the presence of elythra in scaleworms, 2. the type of nephridia, 3, the copulatory apparatus in pisionids.

In respect to the elythra these must be considered as young phylogenetic structures according to Wesenberg-Lund (personal communication). All known pisionids inhabit sandy bottoms and have the slender body common to most animals in these communities. It must be pointed out, however, that there is nothing in the embryonic development indicating an origin of the pisionids from scale-bearing ancestors.

The different types of nephridia seems to form a distinguishing character. The aphroditids have typical metanephridia with an additional function as gonoducts, the pisionids have protonephridia with solenocytes. In the fertile segments a genital funnel has been added to each nephridium and the excretory function is probably depressed. In the fertile segments of the males the distal part of each nephridium forms a copulatory apparatus, in the females a receptaculum seminis is developed. However, it ought to be mentioned that in the aphroditids the main

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part of the segments are fertile and consequently their metanephridia must be compared with those of the genital segments in pisionids, not with the protonephridia in other segments.

Little is known about the propagation in the scale-worms. Many *Harmothoe* species have a brood protection under the elythra where the very young embryos are surrounded by mucus. As a preliminary report from a study in progress concerning the propagation biology of *Pholoe minuta* it ought to be mentioned that at the beginning of the breeding season unfertilized eggs and sperm masses enclosed in a mucus are found adhering to the parapodial bases of the animals. This indicates some kind of pseudocopulation in this species.

b. COMPARISON WITH NEPHTHYDIDAE AND PHYLLODOCIDAE

The family Nephthydidae

When EHLERS (1901) stated a relation to the Nephthydidae he referred to the similar organization of the parapodia and especially to the formation of lobes in the distal ends of the parapodia. ALIKUNHI (1950) pointed out the similar morphology of the nephridia and BANSE (1956) added the possible similarity in the presence of posterior brain lobes. BANSE also pointed out the similar type of larval development.

The doubtful similarity in the parapodia which are biramous in the nephthydids, uniramous in the pisionids, does not seem to favour a connection. The similar nephridia have been discussed above. As regards the posterior lobes of the brain the similarity is highly superficial. In *Pisione* they are the site of the corpora pedunculata; in those *Nephthys* species where they are present they consist of mucus-cells which empty on the lateral sides of the prostomium (CLARK 1955, 1958). The larvae of *Pisione* and *Nephthys* are similar in possessing cup-shaped larval ocelli, many epidermal gland cells in the episphere and a transversal fold between the larval stomach and the intestine. But the *Nephthys* larvae have a teletroch and both in the larvae and in the adults palps are lacking.

The family Phyllodocidae

GRUBE (1857) placed the pisionids among the phyllodocids where he also included the glycerids. AIYAR and ALIKUNHI (1940) pointed out the similar uniramous parapodia and the similar type of nephridia. The latter also makes an attempt to compare the head of *Pisionidens indica* with that of *Eteone*. In both cases there are four slender subulate appendages, but it must be pointed out that in *P. indica* they consist of the palps and one pair of tentacular cirri, in *Eteone* of the two pairs of tentacular cirri which are the only remains of the reduced buccal parapodia. Typical phyllodicids have no palps and no rudiments

are seen in the larval stages. It must be considered as extremely uncertain whether the palps reported in the phyllodocid sub-family Iospilinae are real palps homologous to those of pisionids, aphroditids and nereids. In this aberrant phyllodocid group we also find *Phalacrophorus,* the only genus with an armed pharynx.

In respect to the larval stages there is no special connection between the pisionids and the phyllodocids. But the early trochophore stages of both phyllodocids (Meyer 1938) and aphroditids (Rasmussen 1956, Korn 1958) are provided with a long tuft of immobile cilia asymmetrically on the left side of the episphere. Possibly the very early trochophore of *Pisone remota* has a similar tuft.

c. OTHER ERRANT FAMILIES

As the relations to the families Glyceridae, Hesionidae, and Syllidae (Table 1.) seem to be still more doubtful and as the present writer has no material of these families it is not motivated to discuss them here.

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6. Discussion

a. AFFINITIES

In the comparison with other errant polychaete families many general and detailed similarities have been brought forward which indicate the close relation between the pisionids and the aphroditids. Obviously the pisionids are more related to the genus *Pholoe* than to other groups of the aphroditids. The genus *Pholoe* belongs to the sub-family Sigalioninae (system according to Fauvel 1923). In addition to the material of larvae and adults of *Pholoe minuta* which has been available for the comparison, the writer has also accress to another member of this sub-family, *Leanira tetragona.* Already a preliminary examination of the morphology and histology in the anterior end, especially the nervous system, has shown that *Pholoe* and *Leanira* cannot be more closely related. A future closer examination of the Sigalioninae including members of more genera will probably give as a result that the genus *Pholoe* is excluded from this sub-family.

Besides the affinities of the family Pisionidae there are some details in the development which are worthy of discussion. Firstly we have the relations between the rudiments of the cerebral ganglion and the ventral nerve cord and, secondly we must consider the whole cephalization process. The incorporation of gland cells into the central nervous system will be discussed separately.

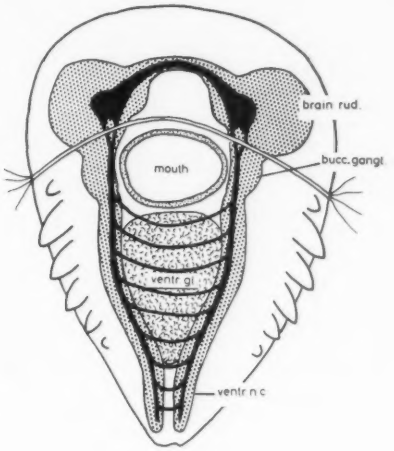

Fig. 24. A scheme of the connections between the brain and the ventral nerve cord in pelagic larvae of *Pisione remota*. The circumpharyngeal connectives are later formed between the buccal ganglia and the rest of the nerve cord.

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b. RELATION BETWEEN BRAIN AND NERVE CORD

In the material available for the present account it has not been possible to follow the earliest development of the brain and nerve cord rudiments. The independent origin of these two structures has been recorded for all species examined. The connection by means of the circumpharyngeal connectives is established very early in actively feeding planktonic trochophores such as *Polygordius, Owenia* and *Pomatocerus* (Woltereck 1905, Wilson 1932, and Segrove, 1941). In yolk-rich forms such as *Scoloplos armiger* this connection develops late in larvae with 12 segments and an age of about 2 weeks (Anderson 1959). In this species the connectives grow out from the brain neuropile and join the nerve cord. This seems to be the generally accepted interpretation concerning the formation of the circumpharyngeal connectives. It agrees with the development observed in the sipunculid genus *Golfingia* (Åkesson 1958, 1961 b). Here the 4 retractor rudiments develop from the dorso-lateral and ventro-lateral margins of the apical plate towards the trunk rudiment. The neuropile of the connectives attach to the ventro-lateral retractor pair.

Both the brain rudiment and the ventral nerve cord rudiment arise in the same way from the ectoderm as the result of a delamination process. In the aphroditid and pisionid larvae the two structures are separated by only the double row of trochoblasts. Judging from the earliest available stages of *Pisione, Pholoe,* and *Harmothoe* the cellular connection under the trochoblast is established in the late trochophore or the earliest metatrochophore stages. Depending on the presence of the ventral gland the halves of the nerve cord are widely separated in the anterior end (Fig. 24). The two halves extend on both sides of the mouth and establish the cellular connection with the brain rudiments. There is no cellular segmental subdivision of the nerve cord in early stages, but the

prospective segmentation is indicated by the commissures. The commissure of the buccal segment forms a bow posterior to the mouth.

When the buccal ganglia move in an anterier direction during the cephalization process the buccal commissure is incorporated into the circumpharyngeal connectives to such an extent that it is not possible to trace it in sections.

c. SEGMENTATION PROBLEMS

Let us now consider the possible segmentation of the brain. The lateral brain rudiments originate in the episphere as undifferentiated cell groups without any traces of a segmentation. The problem of whether the adult brain contains any segmental structures is dependent on whether any ganglia of the ventral nerve cord are added to these epispheral brain rudiments. However, in early stages the buccal ganglia form the most anterior part of the nerve cord. They are closely connected to the brain rudiments by the cell bridges (Fig. 7), but as we have seen, they are not incorporated into the brain. Thus it is obvious that in *Pisione remota* the brain is nonsegmental with the buccal ganglia situated within the brain region but not incorporated.

Recently v. HAFFNER (1959) has given an excellent synopsis of older theories concerning the possible segmentation of the polychaete brain. Also ANDERSON (1959) has entered into a critical discussion of the older segmentation theories. The fundamental problem in all discussions about the organization of the polychaete brain and polychaete prostomium touch upon the question of whether the sub-division of the polychaete brain into forebrain, midbrain and hindbrain, which was originally established by RACOVITZA (1896), has any segmental background, i.e., is the result of a cephalization of segmental ganglia, or whether it must be interpreted as a sub-division purely based on morphological and physiological facts. Both v. Haffner and Anderson maintain the same opinion as the present writer that the polychaete brain is pre-segmental. All supporters of the apprehension that the whole brain is segmental have only studied adult material. Especially the theories of HENRY (1947), RAW (1949), and FERRIS (1953) have ignored all embryological evidence.

Of more interest is the interpretation that the prostomium and the main part of the brain is pre-segmental and that in some polychaetes—not in all—one or more ventral ganglia are secondarily incorporated into the brain. HANSTRÖM (1927, 1928 a,b) has expressed this idea most clearly, but before him it has been embraced by HEMPELMANN (1911), STORCH (1913), HOLMGREN (1916), and others. HANSTRÖM's theory is based largely on the different origin of the stomatogastric nervous system in different polychaete groups. In forms with one or more segmental ganglia incorporated into the brain the stomatogastric nerves originate from the brain proper, in other forms from the connectives or from the suboesophageal ganglion.

A follower of this incorporation theory will find valuable support in the con-

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ditions found in *Pisione remota*. This species can be interpreted as the last stage in this process before the definite incorporation. Considering the strong evidence which has been adduced in the present paper that the pisionids and the aphroditids are closely related, it seems motivated to control the possible incorporation of a segmental ganglion into the brain in the last-mentioned group.

Recently FAUVEL (1959) has published a general synopsis of the polychaetes in Traité de Zoologie (Tome V). Here the nervous system of the anterior end of the aphroditids is represented by STORCH's schematic figure of *Lepidasthenia elegans*. According to STORCH (1912) two fused segmental ganglia are represented by the "commissural ganglia" which are situated on the circumpharyngeal connectives close to the brain. Each ganglion is connected to two podial ganglia, one at the base of the palps and the other at the base of the cephalized segment bearing the tentacular cirri. The podial ganglia are also connected to the brain by a short nerve, which is the last rest of the tetraneure organization. Unfortunately STORCH's scheme does not seem to be representative of the aphroditid nervous system. It has been criticized among others by BERNERT (1926), BINARD and JEENER (1928), and GUSTAFSON (1930). The last-mentioned writer gives a scheme which seems to be more correct. According to this the ganglion of a single cephalized segment is situated at the fusing point of the two connective roots. No ganglion is described from the base of the palps. To summarize all records given by the writers mentioned above, it is obvious that we have no secondary incorporation of segmental ganglia in the aphroditids. STORCH's statement that the palps are the last rudiments of a cephalized segment will be discussed later.

Among the aphroditids and pisionids the cephalization process has not completely reduced the segmental appendages. Bristles or acicula are normally found also in the most anterior segments even if the tactile function is predominating. When we search for polychaete groups with incorporated segmental ganglia, it seems probable that we find them in groups where the cephalized appendages are more reduced than in the two families mentioned above. In the nereids (several authors) and in the phyllodocids (BERGSTRÖM 1914) we can see different stages of a cephalization with respect to the incorporation of the segments with tentacular cirri into the head. But this is not followed by a corresponding cephalization of the nervous system.

The only reason why the present writer will not definitely reject the theory of incorporation and adopt v. HAFFNER's assertion, that such an incorporation has never been observed in the polychaetes, is the condition found in early planktonic stages of *Tomopteris helgolandica*. Here the first two segments are setigerous. During the development the first segment becomes successively reduced and the corresponding ganglion seems to disappear. In the youngest collected stages with 4—6 segments this ganglion has not only a pre-oral but also a pre-cerebral position. However, it is not possible to evaluate these observations before the cephalization process has been studied in still younger larvae.

d. THE CONCEPTION OF PALPS

The origin of the palps in polychaetes has often been discussed and a correct definition of the palps has been wanted in order to separate them from antennae, oral lips, tentacular cirri, and other appendages in the anterior end. A survey of older interpretations is given by GUSTAFSON (1930). Recently v. HAFFNER (1959) has discussed the morphological difference between the palps and the antennae in *Hyalinoecia* and other eunicid genera. He could show that some eunicids are erroneously described as having seven antennae, the two small frontal antennae originating by division of the palps. Unfortunately it can be doubted, however, whether these structures described as palps in the eunicids are real palps or whether they are homologous to the oral lips in the family Amphinomidae. According to STORCH (1913) three different structures are described as palps: 1. The palps of the amphinomids and eunicids, which are ventral evaginations of the head ectoderm. They are diffusely innervated from the frontal part of the brain. 2. The palps of the aphroditids, which are stated to belong to a cephalized segment. They are innervated from the lateral parts of the brain. 3. The palps of the spionids, which clearly belong to the first segment.

The family Pisionidae belongs to the second group as also the Syllidae, Hesionidae, and Nereidae (GUSTAFSON 1.c.). In agreement with BINARD and JEENER (1928) GUSTAFSON states that in all errant polychaetes the antennae and the palps are homologous. This had been stated much earlier by CLAPARÈDE (1868), who considered the palps as specialized antennae.

If embryological evidence is taken into consideration these postulated homologies between palps and antennae are pronouncedly contradictory to another statement that the palps are derived from the first segment, i.e., a segmental component in the brain. This statement is put forward among others by HEMPELMANN (1911), STORCH (1913), and BINARD and JEENER (1.c.). SÖDERSTRÖM (1920) states the same for the spionids, but here we have another type of palps. In his classic paper KLEINENBERG (1886) stated that in *Lopardorhynchus* not only the paired lateral antennae but also the unpaired median antenna originate from paired cell groups in the episphere. Thus if palps and antennae are homologous the former cannot be derived from a somatic segment. But as we have seen in the present paper the palps of *Pisione remota* have an origin quite different to that of the antennae. In this species there are no antennae, but the origin of these structures is well known not only from KLEINENBERG's investigations but also from the descriptions given by KORN (1958) and others. After having controlled the formation of the palps in a number of aphroditid and nereid species the present writer has been convinced that the palps are diffentiated in the same way in all polychaetes belonging to STORCH's second group. Therefore, it seems convenient to give a definition of palps which is based upon embryological evidense and is valid for the errant polychaete groups mentioned above. Thus the palps are de-

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fined here as paired structures with a double origin. The formation is initiated by the mesodermal part, which originates from the mesenchyme of the pharynx region and grows between the two connective roots into the undifferentiated brain rudiment. One ectodermal part forms the external cover of the palp. There is no connection with any segmental structure.

Starting from the embryonic conditions the divergent observations about the innervation of the palps is easily understood. In the forebrain-, midbrain-, and hindbrain-scheme according to RACOVITZA (1896) the palps belong to the forebrain. This is interpreted as a morphological differentiation associated with a pair of sensory organs, the palps. The palp nerve is connected both with the two connective roots and with the brain where the two sides are connected by a strong palp commissure.

According to HANSTRÖM (1.c.) and others the ganglion of the buccal segment has been incorporated into the forebrain in those forms where the stomatogastric nerves are given off from the brain. But in *Pisione remota* these nerves are given off from the connectives caudal to the buccal ganglion. This will upset the interpretation of *Pisione* as representing a stage just before the incorporation of the buccal ganglion. The present writer is inclined to accept V. HAFFNER's opinion, that in the polychaetes the stomatogastric nerves have not yet become so fixed with respect to their origin as in the arthropods.

e. GLANDULAR AND NEUROSECRETORY STRUCTURES

Recently CLARK (1956 a and b) has discussed the origin of the neurosecretory cells. Against HANSTRÖM (1954) he maintains the opinion that neurosecretory cells more than other nerve cells have maintained the secretory ability which is a fundamental property of all ectodermal cell. He also gives some exemples from the families Nephthydidae and Nereidae, from the nemerteans and the crustaceans that epidermal gland cells have become incorporated into the central nervous system. The present writer (ÅKESSON 1961 b) has been able to follow an incorporation process of glandular epidermal structures in the sipunculids. The abundance of gland cells in the episphere in *Pisione remota* corresponds to the conditions observed in other polychaete larvae (HEMPELMANN 1911, KORN 1958). In his discussion of these epidermal gland cells in larvae of *Harmothoe imbricata* and *H. impar* and of the neurosecretory cells in the adult brain of the same species KORN has used an inconsistent terminology with respect to the names of the larval structures. Epidermal gland cells with a superficial position and no true connection with the brain rudiments according to the present writer's control on the available material of *H. imbricata* are alternatingly called gland cells and neurosecretory cells. CLARK (1956 a) has given a definition of neurosecretory cells which summarizes the discussion of SHARRER and SHARRER (1954): "Neurosecretory cells are defined as cells which have the morphological characteristics of neurones: axon, neurofibrillae and Nissl bodies, and which secrete a

substance that aggregates in droplets or granules so as to be microscopically visible in living or suitable stained material." These demands are presumably not fulfilled in all described neurosecretory cells from polychaetes, but the cells must at least be situated within the nervous system.

In *Pisione remota* the ventro-median glandular complex just anterior to the prototroch is not incorporated into the brain. The cells are disintegrated during the metamorphosis and their last rests are visible in the most anterior part of the head in juvenile bottom stages (Fig. 18). But the originally superficial gland cells close to the median pair of eyes sink down and are incorporated into the brain. In the adults they are visible as a well delimited glandular area ventral to each eye in the middle part of the posterior lobes. These cells have retained the rounded appearance of the epidermal gland cells. In the available material no axones and no secretory transmission have been observed. But as the cells have a position close to the ventro-lateral surface of the brain, it cannot be excluded that they are functional neurosecretory cells which empty the secretion into the coelome.

The cells of the prominent ventral gland disintegrate during the metamorphosis. The nuclei of some of these cells are seen within or close to the neurones of the nerve cord even after the metamorphosis. However, the fate of these nuclei is unknown.

In polynoids, such as *Harmothoe imbricata, H. impar* and *Pholoe minuta,* the corresponding rudimentary gland is situated in the most posterior part of the nerve cord region. A few cells surround the narrow opening, which is situated on a ciliated field.

In the youngest collected larvae of *Pholoe minuta* the mid-ventral cells anterior to the glandular area differ from the surrounding neurones in being secretory (Fig. 23). In other respects they are typical nerve cells. In older larvae the cells of this region are not distinguishable from the surrounding nerve cells. ANDERSON (l.c.) reports gland cells which later disappear in the nerve cord of *Scoloplos armiger*. In all these cases the fate of the cells is unknown, but they furnish good evidence that an incorporation of glandular structures into the central nervous system is of common occurrence.

7. Summary

Metatrochophores of *Pisione remota* were collected from the plankton. Some of them were reared and brought to the metamorphosis. Bottom stages and adults were collected from the sand.

The planktonic larvae are of the same general type as aphroditid larvae. They have a prominent ventral gland which opens on a caudal stylus. The secretion from the gland forms a collecting apparatus, a slime net to which the food par-

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ticles adhere. Reserve food is accumulated in the endoderm cells during the planktonic life.

The metamorphosis involves a far-reaching transformation of the anterior end. For at least two days the mouth is closed and the larva must live on the stored reserve food. The segment number is constantly 8 both in the last stages of planktonic life and during the metamorphosis. New segments are not added before the anterior end has been transformed into the adult organization.

The cerebral ganglion arises from two ventro-lateral rudiments, which have a cellular connection with the anterior end of the ventral nerve cord in the earliest collected larvae. This cell bridge is retained to the metamorphosis. During the metamorphosis the cerebral ganglion detaches from the epidermis and extends as two free posterior lobes to the level of the fifth segment. These lobes contain the corpora pedunculata. Some gland cells from the episphere of the metatrochophore are incorporated into the brain with retained secretory properties.

In the last pelagic stages and during the metamorphosis the buccal appendages move towards the anterior end. The parapodia proper are reduced and are only represented by stout acicula and podial ganglia. The dorsal cirri have developed into slender tactile organs, the ventral ones are flask-shaped.

The palps have a double origin. The mesodermal central part arises from lateral cell groups which are associated to the pharynx rudiment. Such a mesoderm bud grows between the two roots of the circumpharyngeal connective into the undifferentiated cell mass of the brain rudiment. The mesoderm is demarcated by a connective tissue sheath.

The pharynx is differentiated from the inner part of the stomodaeum and from a surrounding layer of mesoblasts which have probably an ectomesenchymal origin. These mesoblasts give rise to the radiating muscle layer.

The ventral gland and the stylus disintegrate during the metamorphosis.

The development of the nervous system gives no evidence of a segmentation of the brain. The brain proper arises from the two lateral rudiments in the episphere and must be considered as pre-segmental. The buccal ganglia are cephalized but not incorporated with the brain. The same conditions are met with in the nereids, aphroditids and phyllodocids.

A comparison with larvae of other errant polychaetes yields strong evidence that the pisionids are more closely related to the aphroditids than to any other group. Among the aphroditids *Pholoe minuta* exhibits the closest connection with the pisionids.

This investigation has been supported by the faculty of Mathematics and Natural Science of the University of Lund, the Royal Physiographical Society of Lund, and the Swedish Natural Science Research Council, Stockholm.

8. Abbreviations

akr.	akrotroch
brain rud.	brain rudiment
bucc. ac.	buccal aciculum
bucc. gangl.	buccal ganglion
bucc. par.	buccal parapodium
bucc. reg.	buccal region
conn.	circumpharyngeal connective
d. c. I	dorsal cirrus of the buccal segment
d. c. II	dorsal cirrus of the second segment
end.	endoderm
epid.	epidermis
gl. c.	gland cell(s)
intest.	intestine
lat. eye	lateral eye
med. eye	median eye
nephr.	nephridium
neur. ac.	neuropodial aciculum
not. ac.	notopodial aciculum
palp mesod.	palp mesoderm
palp retr.	palp retractor
palp rud.	palp rudiment
pap.	papilla
par. II—VI	parapodia of the II—VI segments
phar.	pharynx
phar. g.	pharynx ganglion
phar. rud.	pharynx rudiment
pod. g.	podial ganglion
post. lobes	posterior lobes of the brain
pr. g.	"prostomial ganglion"
prot.	prototroch
prot. mu.	prototroch muscle
prot. n.	prototroch nerve
rad. mu.	radiating muscle layer
stom.	stomach
stom. n.	stomatogastric nerve
stomod.	stomodaeum
transv. fold	transversal fold
vac.	vacuole
v. c. I	ventral-cirrus of the first segment
v. c. II	ventral cirrus of the second segment
ventr. gl.	ventral gland
ventr. n. c.	ventral nerve cord

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Cone Types and Cone Arrangement in the Retina of Some Gadids[1]

by

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(Received 7th June 1961.)

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Introduction

In spite of the family Gadidae being a large and widely distributed group of fishes representing many different modes of life, the visual cells of the family are very poorly known. In the genus *Gadus,* the best known species is *Gadus callarias.* NUNNELEY (1858) evidently noticed some kind of double cone elements in this species, but did not give any exact definition. COBBOLD (1862) clearly figures twin cones with equal halves and also reports single cones. According to FRIIS (1879) this species has only twin cones ("tvillingetapper"), but as he does not distinguish between equal and unequal double cones, this term does not necessarily mean equal double cones. KRAUSE (1886) mentions "Zwillingzapfen" in this species, and LYALL (1957 b) states that it has "almost exclusively double cones", without further definition of the character of these elements. He makes

[1] Aided by grants from Statens naturvetenskapliga forskningsråd.

the same statement as regards *Gadus merlangus*. According to WALLS (1942) *Gadus polachius* has only twin cones.

In the genus *Merlucius*, *M. merluccius* has, according to FRIIS (1879), both "twin cones" and single cones, and he notes as especially remarkable that there also exist single cones which are small and slender, as if they were not fully developed.

The eelpout, *Lota lota*, is known from WUNDER (1925, 1926) to have very few cones in relation to the number of the rods. However, the character of the cones is not mentioned by WUNDER, and the statement made by HANNOVER (1843) that this species has "twin cones" is the only indication that such elements are present. In the drawing found in MENNER (1929), only single cones can be seen.

As WALLS (1942) points out, a close examanition of the cone types and the cone mosaic of the Gadids should be of great interest. Thus one would obtain a valuable contribution to the discussion on the evolution of the different types of double cone elements. In view of the above-mentioned lack of such investigations, I have examined 10 Gadid species in respect of their cone types and cone mosaic.

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Material and Methods

In my previous work as well as in the material now presented, I have not found any individual variation necessitating a great number of individuals of every species. Consequently, in order to limit the purely technical work, I have, as a rule, only examined 2—3 specimens of each species, sometimes more, sometimes only one. The following species were examined:

Gadus callarias	5 specimens	(70—660 mm)
Gadus pollachius	2 "	(210—360 ")
Gadus aeglifinus	3 "	(250—300 ")
Gadus merlangus	3 "	(25—220 ")
Gadus esmarckii	2 "	(150—170 ")
Gadus minutus	2 "	(155—210 ")
Merlucius merluccius	2 "	(400—410 ")
Gaidropsarus mustelus	1 "	(230 mm)
Raniceps raninus	2 "	(230 mm)
Lota lota	5 "	(150—470 mm)

The eyes were fixed in Bouin's fluid and then treated in the way described in my last paper (ENGSTRÖM 1960).

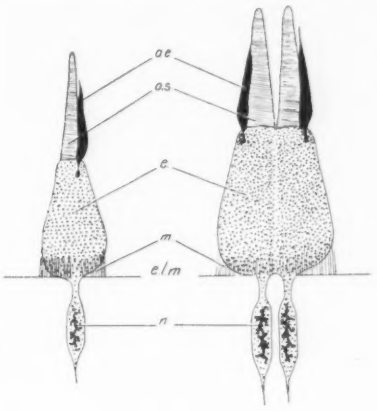

Fig. 1. A, single and B, double cone of *Gadus callarias*, representing the cone types in the more central areas of the eye. a. e. = "accessory elements" (see text), o. s. = outer segments, e. = ellipsoids, m. = myoids, e. l. m. = external limiting membrane, n. = nucleus.

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Results

1. THE CONE TYPES

The genus Gadus

When studying the different species, I have been able to establish that the variations between the species are very insignificant, and they have therefore been treated together. In all the species examined, it has been possible to establish the presence of single as well as of double cones.

The single cones

A single cone from *Gadus callarias* is pictured in fig. 1. A noteworthy formation which I have not found mentioned in the literature but which is to be found in all these species, is the accessory element which is to be seen beside the outer segment. In a section with unbleached pigment it may, on account of the surrounding pigment, be difficult to detect, but after bleaching in Potassium permanganate and Sodium bisulfite, it stands out clearly, as it is easily stained, e.g. in Regaud's Haematoxylin.

In *Gadus callarias*, this accessory element is quite prominent with its narrow base attached to the ellipsoid, just at the transition between this and the outer segment. Just outside the attachment it thickens and then follows closely along the outer segment, gradually narrowing. Its outermost part narrows quickly into a very thin thread, the end of which cannot be distinguished with certainty. I have not been able to ascertain whether it ends in this point, inside that of the outer segment, or whether it may possibly continue as a very thin thread up towards the pigment layer. In some slides, something which may be interpreted to this effect has been seen, but among the rods and the processes from the pig-

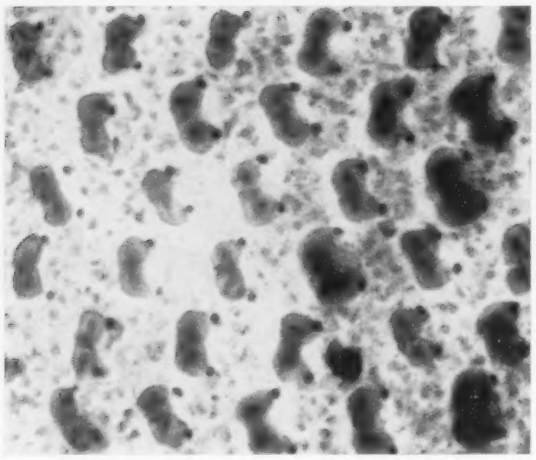

Fig. 2. Tangential section of the retina of *Gadus esmarckii* at the level of the twin cone outer segments. The dark points close to the paired outer segments are the "accessory elements". Foot-Masson (pigment bleached), 6 μ, 930 ×.

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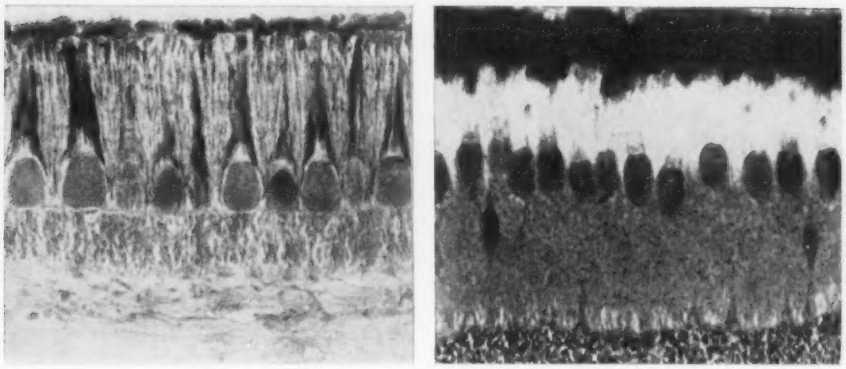
ment epithelium, it has not yet been possible to find out the continuation of this very tiny prolongation—if there is any. Quite naturally, nothing can as yet be settled as to the function of this formation, since for this more thorough investigations are necessary.[1]

The form of the single cones can be the slightly elongated pear-shaped one shown in fig. 1, or it may be a little more slender in some species. This applies to the central regions of the retina. The cones newly formed near ora serrata are more slender and have more elongated outer segments and thinner, threadshaped accessory elements. The most prominent part of the cone is the ellipsoid, which, in the light-adapted eye, is in direct contact with the external limiting membrane. The moyid, in that condition, is not easily discerned and is seen only as thin threads surrounding the base of the ellipsoid. The elongated cone nucleus is seen among the rod nuclei inside the external limiting membrane. In all species, the single cones stain a little more heavily than the double cones.

The double cones

As seen in fig. 1, the two halves of the double cones are quite identical; they are in other words typical twin cones or equal double cones. The twin cones, too, have these special "accessory elements" described in the single cones, one on each half. They are not always as thick as in *Gadus callarias*, but vary in thickness in the different species. They are at their thinnest in *G. esmarckii*, where the thin threads, gradually narrowing, closely follow the outer segments. In a tangential section of the retina, one can see that they are also very regularly arranged

[1] Preliminary electron microscopic studies have now revealed that this accessory element has a ciliary base of the type as the connecting cilium of the outer segment.



A B

Fig. 3. The retina of *Gadus callarias*, A, light-adapted, B, dark-adapted. Foot-Masson, 6 μ, 280 ×.

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(fig. 2). As will be shown below (pp. 234 ff.), the twin cones are regularly arranged in rows, their long diameter being normally disposed at right angles to the radius. The accessory elements are regularly found on the side of the outer segments turned towards the centre, as is shown in fig. 2.

The twin cone pictured in fig. 1 represents the light-adapted cones in the more central area of the eye. Here the outer segments are relatively short and thick and the ellipsoids are quite bulky. From the base of the outer segment and along the ellipsoids, the two halves of the twin cones are very intimately joined. In many sections it is very difficult to see any limit at all, but mostly this appears as a light line. Sometimes, one of the halves has stained very heavily while the other has stained normally (cf. fig. 5). In some species, the limit may be seen a little more easily, but the difference between the species is very insignificant and may also be due to how well the material has been fixed. As in the single cones, the ellipsoids touch the external limiting membrane, the myoids being seen only as thin threads around the base of the cone. The two nuclei of the twin cone are elongated and are to be found among the rod nuclei, on the same level as those of the single cones.

Like the single cones, the twin cones near ora serrata are small and have long and slender outer segments. Towards the centre of the eye, they at first grow long and slender with long outer segments and filamentous accessory elements, then more and more bulky and about half-way towards the centre, they have gained the appearance figured in fig. 1.

Triple cones

Triple cones have been found in four *Gadus* species. In *G. minutus* and *G. merlangus* they are found very occasionally, in *G. pollachius* a little more fre-

quently and in *G. aeglifinus* a little more frequently still. In these triple cones, the three components nearly always form a triangle, and they differ in this respect from those described by VRABEC (1955) in some Cyprinids and those described by LYALL (1957 b) in *Salmo* and *Phoxinus*. In these fishes, the three cones of a triple cone were found to be arranged in line, and I have also observed the same type of triple cones in my own Cyprinid material.

The dark-adapted retina

The cones described above are, as has been pointed out, those of the light-adapted eye. As the myoids of these cones are very inconspicuous, it would seem desirable to find out whether these cones are able to perform any photomechanical changes. I have therefore totally dark-adapted four eyes of *Gadus callarias* by keeping the fishes in total darkness for two hours before the fixation of the eyes, which was also performed in darkness.

In the light-adapted eye, the processes from the pigment epithelium extend into the spaces between the ellipsoids. Both around the single and the twin cones, they form especially tight bundles, which like sheaths enclose the outer segments. The rods are totally enclosed in the pigment (fig. 3A). In the dark-adapted eye (fig. 3B), the pigment is redrawn and concentrated near the pigment epithelium, the rods are found near the external limiting membrane, and the cones are found outside the rods. The myoids of the cones are thus found to be very elastic, those of the twin cones being most stretched.

Merlucius merluccius

The single cones are mainly of the same type as those of the *Gadus* species described above as regards the myoid and the presence of the accessory element. However, this element is narrow and filamentous and follows the outer segment closely. There is also a certain variation in the form of the ellipsoids of the single cones—some of them are quite thick, but others are very thin. All the single cones stain much more heavily than the twin cones in the Foot-Masson trichrome staining.

The twin cones are in all respects very similar to those of the genus *Gadus*. Even in the twin cones, the accessory elements are very thin and filamentous. Some triple cones have also been found in this species.

Gaidropsarus mustelus

In this species, the cones differ a little from those of the species described above. The single cones are not especially slender or small, but correspond roughly to one half of a twin cone. The twin cones are not so bulky and not so

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intimately united as those of the species already mentioned, but one can see a distinct limit between the two halves. In a tangential section, this limit is clearly seen, the twin cones having the outlines of an "8" (cf. fig. 7). The two halves are not always quite identical, but one can often see twin cones where the one half appears somewhat shorter than the other (fig. 4 A). The myoids are clearly visible between the ellipsoid and the external limiting membrane, at the inner side of which the cone nuclei are to be found. In both single and twin cones, narrowly extended accessory elements are found.

Triple cones are not infrequent and are arranged in the form of a triangle.

Raniceps raninus

The cones of this species also differ in some respects from those of the *Gadus* and *Merlucius* species described. The shape of the single cones varies a little, but in general they are a little shorter than the double cones, elongated, pearshaped, and about as thick as one half of a double cone. A thin accessory element is found along the outer segment. The nucleus, as in the other species mentioned, is elongated and situated inside the external limiting membrane.

As in *Gaidropsarus,* the double cones are not always to be regarded as typical twin cones, the two halves very often being of different length. Neither are they as closely jointed as in *Gadus,* but are otherwise built like the *Gadus* twin cones. They, too, have thin accessory elements along the outer segments, and the elongated nuclei are also in the double cones situated inside the membrane. Triple cones are found relatively often, all of triangular shape.

Lota lota

As in *Gaidropsarus* and *Raniceps,* the cones of the eelpout are not exactly of the *Gadus* type. The single cones are of about the same length as the twin cones, of uniform thickness and a little narrower than one half of a twin cone. Neither in this species are the double cones typical twins. As in *Gaidropsarus* and *Raniceps,* one of the halves will often seem to be a little longer than the other. This seems to be the case in the light-adapted eye (fig. 4 C), but after dark-adaption, when the cones have migrated towards the pigment epithelium, one can see the shape of the twins more easily. It will thus be clear that the two halves are not unequal in length, but that the ellipsoids do not quite correspond (fig. 4 D). The cones thus tend to be similar to the unequal double cones of the Cyprinids (Engström 1960) or those of the Holosteans (Walls 1942).

Triple cones have been found to be regularly present.

In all types of cones, the accessory elements have been observed as thin, threadshaped strains along the outer segments.

The cone nuclei are not as elongated as in all the previous species, but are more

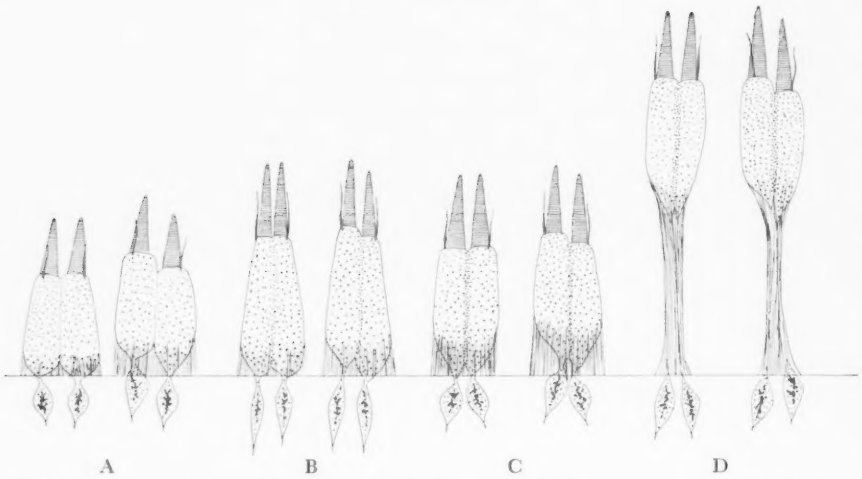

Fig. 4. Diagram of the double cone elements of A, *Gaidropsarus mustelus*, B, *Raniceps raninus*, C, *Lota lota*, light-adapted, and D, *Lota lota*, dark-adapted. In all these species there exist both identical twin cones and slightly unequal double cones, the form of which is best seen in the dark-adapted retina (D).

bulky and vary a little in their proportions. They also vary in their position; mostly they are to be found inside the external limiting membrane, but often they penetrate the membrane and sometimes they can be found outside it.

2. THE CONE MOSAIC

From eyes of all the species treated in this paper, I have cut out small pieces of the retina from the regions dorsal, ventral, temporal and nasal to the optic disc, and the origin of these pieces have been mapped. The pieces are sectioned tangentially and from these sections the arrangement of the cones has been studied. The diagrams are obtained as described in an earlier paper (ENGSTRÖM 1960), i.e. the deviations from the ideal position of the twin cones (90° to the rows) are plotted in the diagram in groups of 5°.

The genera Gadus and Merlucius

In all species of the genus *Gadus*, the twin cones are arranged in rows, mainly following the radii of the eye. In these rows, the twin cones are regularly arranged with their long diameter at about right angles to the rows (fig. 5). The single cones are not arranged regularly in relation to the twin cones, but are scattered among them in varying numbers, always relatively few in relation to the twin cones. The pattern will also be seen in tangential sections through the layer of the pigment epithelium processes of the light-adapted eye where the clustered processes enclosing the cones can be clearly observed.

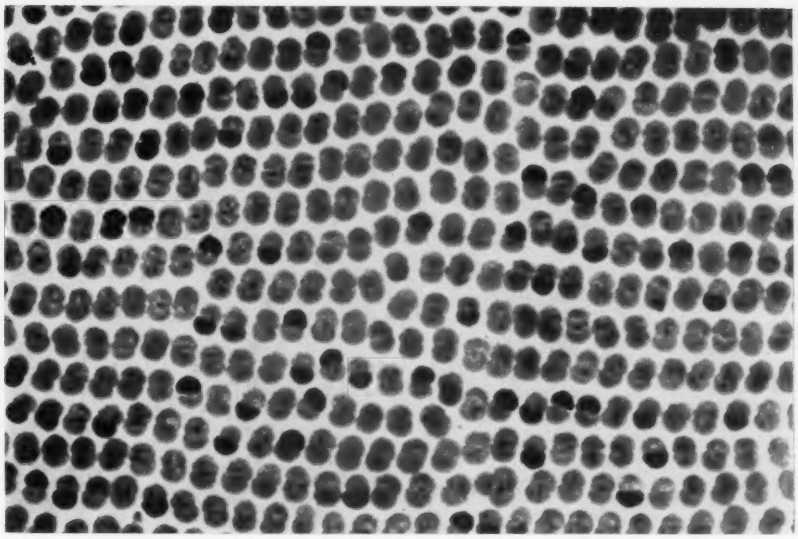

Fig. 5. Tangential section of the retina of *Gadus minutus*, temporal to the optic nerve, showing the regular arrangement of the twin cones into rows. Foot-Masson (pigment bleached), 6 μ 400 $\times$.

In its essential characteristics, the pattern thus resembles that of the Cyprinids described in an earlier paper (ENGSTRÖM 1960), disregarding the fact that the single cones in the Gadids are present only in small numbers and are scattered instead of being arranged in rows. This pattern, however, also resembles that of the Cyprinids in another respect, i.e. its variation in regularity between the different regions of the eye. However, this variation is not at all as conspicuous in the genus *Gadus* as in the Cyprinids. Only a slight tendency to a more regular pattern in the equator of the eye can be traced in some *Gadus* species, but in e.g. *G. pollachius* no such variation has been found (fig. 6). On the other hand, a pronounced difference in the density of the visual cells can be noticed. In the eye figured in the diagram in fig. 6, the number of twin cones per sq. mm (counted in tangential sections) was in A (temporal) 14.800, in B (nasal) 2.800, in C (dorsal) 3.300 and in D (ventral) 4.800. Thus a pronounced concentration in the temporal part of the equator of the eye can be seen, i.e. the same region which was found to have the most regular pattern in the Cyprinids.

The most regular patterns in the genus *Gadus* are found in *Gadus esmarckii* and *Gadus minutus* (fig. 7), where the rows are very exact, and the twin cones very strictly arranged. In *Merlucius*, the cone arrangement is found to be the same as in Gadus, and the variations between the different regions of the eye are very inconsiderable.

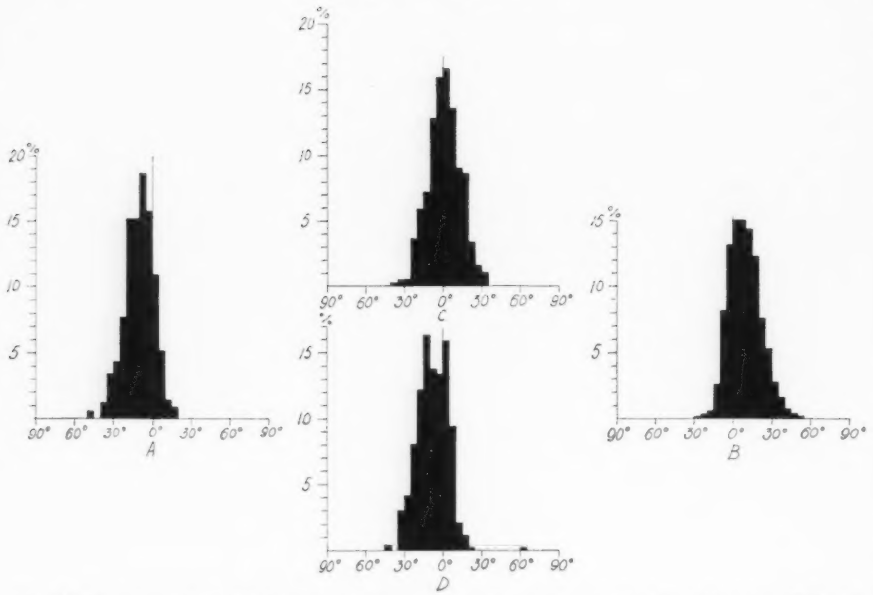

Fig. 6. Diagrams of the twin cone arrangement in the retina of *Gadus pollachius*, 360 mm, showing the very regular orientation of the twin cones (see text). A, temporal part of equator (350 twin cones measured), B, nasal part of equator (553 twin cones), C, dorsal (392 twin cones) and D, ventral part of the retina (436 twin cones). All measurements about 5 mm from the optic nerve.

Gaidropsarus mustelus

The cones of *Gaidropsarus* are not at all as regularly arranged as in *Gadus* and *Merlucius*. The cones occur more sparsely than in these species, and at a first glance at a tangential section, they seem to be haphazardly distributed (fig. 7). However, an analysis of the angles of the double cones to the radii will show that a certain arrangement can be found. In the diagr. in fig. 8, there is a clear concentration of the angles measured towards one point of those diagrams representing sections from the horizontal equator of the eye. Such a clear concentration cannot be traced in the diagrams representing the dorsal and ventral regions of the retina, even if there might be a slight tendency in the ventral region. This will mean that, in the equator of the eye, the twin cones tend to be arranged in something like the regular rows of the Gadus species. It may seem a little confusing that the most pronounced concentration is sometimes not found around the centre of the diagram. This is due to the fact that the rows of twin cones sometimes change their direction in relation to the radii of the eye. A right angle to the row does not therefore always mean the same angle to the radius, but as the main purpose of the diagram is to find out whether there is any tendency to concentration, it will be less important at what angle this concentration is found.

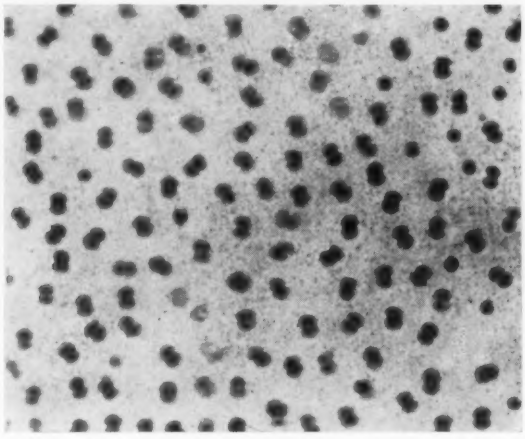

Fig. 7. Tangential section of the retina of *Gaidropsarus mustelus*, temporal to the optic nerve (corresponding to diagr. A, fig. 8), showing an apparently irregular position of the twin cones. Foot-Masson (pigment bleached), 5 μ 340 ×.

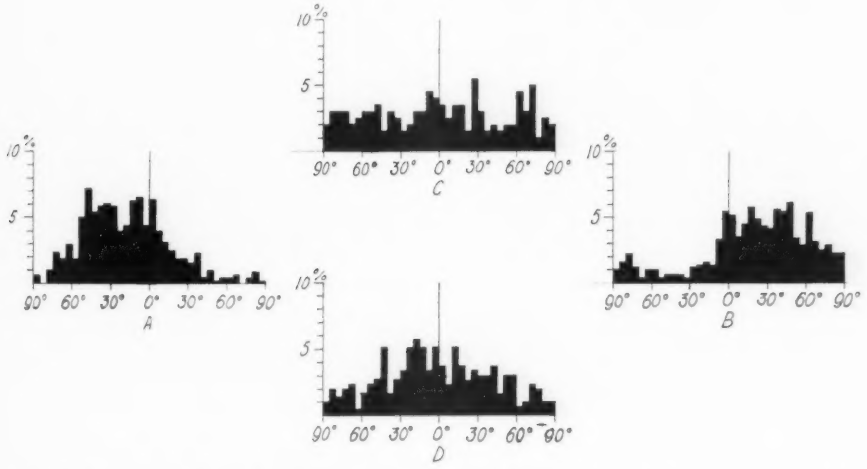

Fig. 8. Diagrams of the double cone arrangement in the retina of *Gaidropsarus mustelus* (230 mm), showing a tendency to more regular organization along the equator than in the dorsal and ventral regions. The same regions as in fig. 6. A, 477, B, 625, C, 200, D, 295 double cones. All measurements about 2 mm from the optic nerve.

Raniceps raninus

Also in this species, the pattern seems, at a first glance, to be totally dissolved. In the diagrams, however, a clear tendency to concentration towards the centre of the diagram will be seen (fig. 9). Any tendency to a more regular pattern along the horizontal equator of the eye can not be traced in these diagrams.

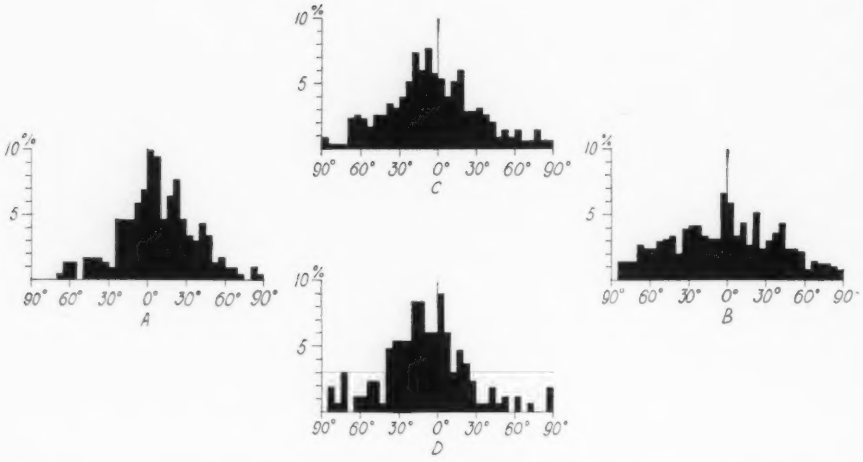

Fig. 9. Diagrams of the double cone arrangement in the retina of *Raniceps raninus* (230 mm). The same regions as in figs. 6 and 8. A, 234, B, 411, C, 350, D, 167 double cones. All measurements about 2 mm from the optic nerve.

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Lota lota

In the specimens 150 mm in length, the patterns was found to be rather regular and of the same type as that of *Gadus* (fig. 10). The most regular arrangement was found near the margin of the retina; in the more central region, the arrangement was not so regular, but definite rows with the twin cones regularly arranged were found here, too (fig. 11). In more grown-up individuals (450 mm), the arrangement is not so easy to discover. Along the equator, the arrangement in rows can be distinguished, but in the dorsal and ventral regions one cannot with certainty recognize the pattern. In a diagram, however, the tendency to a pattern of the Gadus type will be clearly traced.

3. THE RODS

In all the species described in this paper, rods are very numerous. Although I have not studied them at all thoroughly, I want to give an account of a few observations.

In the dark-adapted eyes, where the processes from the pigment epithelium are redrawn and the rods have migrated towards the external limiting membrane, one can, in tangential sections, see that also the rods have the accessory elements described above in connection with the cones of all the species mentioned. In these sections, they will be seen as dark points close by the outer segments. This means that they lie like thin threads along these outer segments, but they are

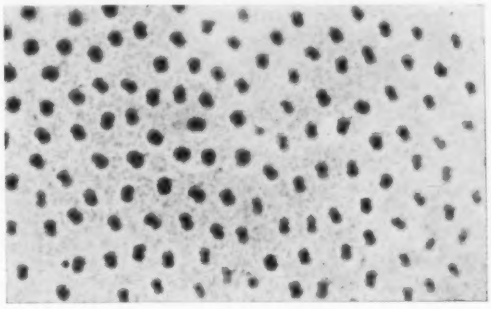

Fig. 10. Tangential sections from the retina of *Lota lota* (150 mm), corresponding to diagram A in fig. 11. Foot-Masson (pigment bleached), 5 μ, 350 $\times$.

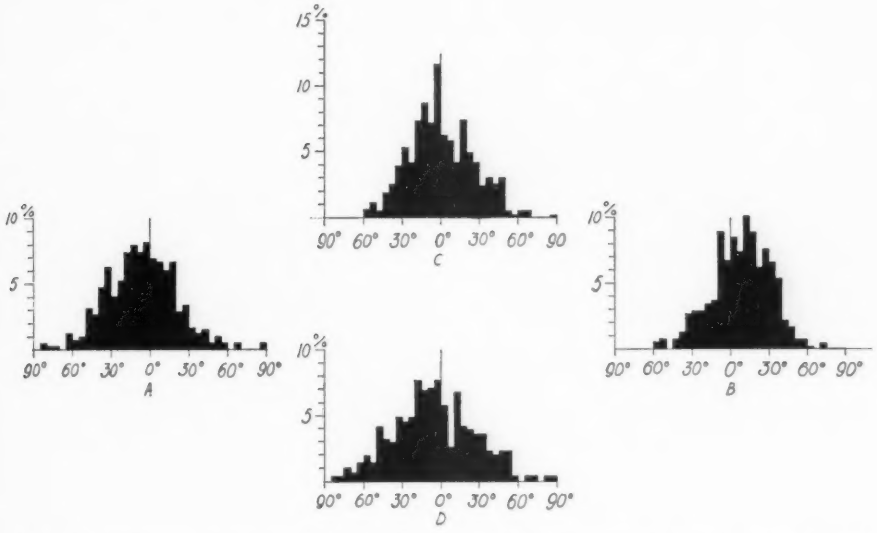

Fig. 11. Diagrams of the double cone arrangement in the retina of *Lota lota* (150 mm). All measurements about 1.5 mm from the optic nerve. A, 418, B, 567, C, 437, D, 312 double cones.

very difficult to observe in transverse sections of the retina and especially in unbleached ones from light-adapted eyes, where the pigment covers the rods.[1]

[1] After having found that these accessory elements are present in all the visual elements of all species examined in this paper, I have examined a number of species representing different other groups of fishes. These elements are actually present in all Cyprinids described in a previous paper (Engström 1960), as well as in all examined species in a material of Percomorph fishes, and in some other fishes. The element thus seems to be a regular component in the visual cells of fishes, although they are nowhere found so well developed and so conspicuous as in some of the Gadids.

Discussion

As stated in a previous paper (ENGSTRÖM 1960), there exist different opinions as to whether the cone types and the cone mosaic are dependent on the phylogeny of the fish or are only a result of ecological adaptation. In the Cyprinids, I found both the cone types and the mosaic in which they are arranged to be of fundamentally the same type with only certain variations between the species. In this paper, I have examined ten species of the family Gadidae in order to find out whether this uniform organization within a systematical unit is to be considered the rule and not merely a consequence, in the case of the Cyprinids, of the relatively similar modes of life of those species of the family which I described. The Gadid species examined represent more varying modes of life—some more or less deep-going marine species (*Gadus, Merlucius*), some species living near the bottom in shallower water (*Gaidropsarus, Raniceps*), and also a bottom-dwelling fresh-water species (*Lota*), often found in shallow water and with predominantly nocturnal habits. The visual cells of the Gadids might also be of special interest with regard to their uncertain phylogeny.

As has been shown above, the Gadid species studied are fundamentally similar as regards both the cone types and the cone arrangement. In all the *Gadus* species as well as in *Merlucius,* there is hardly any difference in shape between the cones. They all have perfect twin cones with the same type of bulky ellipsoids, tightly grown together, and myoids which in the light-adapted eye are not visible between the ellipsoids and the external limiting membrane. In *Gaidropsarus, Raniceps* and *Lota,* to be sure, the twin cones are not as regular as in the *Gadus* and *Merlucius* species, but in other respects they are of fundamentally the same type. The "accessory elements", the function of which is diffucult to understand, are also found in some form in all the species examined.

The cone types of the Gadids have been regarded by WALLS (1942) as essential for the solution of the problem of the origin of the twin cones. He points out that a difficulty as regards the deduction of the twin cones of the Gadids is the uncertain origin of these fishes. Supposing that they should be related to the Coryphaenoidid fishes, the problem is that these fishes have only rods (WALLS 1942). This does not necessarily mean, however, that the Gadids have invented twin cones for themselves. Instead, it might be explained by the Coryphaenoidids and the Gadids having developed from a common ancestral group equipped with double cone elements of some kind. In the Gadids, these elements may have been transformed into twin cones; in the Coryphaenoidids they might have disappeared totally. However, the systematical position of the Coryphaenoidid fishes is far from obvious, and it is not necessary to consider them to be of the order Gadiformes. SVETOVIDOV (1937) and BERG (1958), for instance, range them in a separate order, the Macruriformes, and the phylogenetic relations

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between the two orders can be considered to be uncertain. BERG (1958) regards the order Gadiformes as a primitive order, which in late Cretaceous emerged from fish types related with the extinct family Pachycormidae. About the visual cells of these fishes nothing is, of course, known, but as the holostean fish *Amia*, one of their most closely related recent ancestors, is known to have a certain kind of double cones (WALLS 1942), it may seem possible that also the Pachycormidae were equipped with double cone elements of some kind. In that case, the existence of twin cones in the Gadidae can be explained as a further development of these double cones. Perhaps the above-stated irregularity in the composition of the twin cones of *Lota, Gaidropsarus* and *Raniceps* might be considered to be a relic from their developing from double cones. WALLS, it is true, considers it possible that the teleostean unequal double cones may be the result of a secondary derivation from twin cones. In this case, however, such a hypothesis may not be necessary, as at least *Lota* is generally regarded as having long ago become separated from the other Gadids (e.g. GRASSÉ 1958) and the irregularity of its twin cones will thus be naturally explained as a relic from a double cone stage. In this connection it may also be pointed out that the nuclei of the twin cones in this species often penetrate the external limiting membrane as do also those of the double cones of *Amia*.

As regards the cone mosaic, MÜLLER (1952) has studied the formation, in *Lebistes*, of the mosaic during the histogenesis, and LYALL (1957 a, b) has carried out a corresponding investigation in *Salmo, Phoxinus* and some other species. They have both established that the cone pattern is formed at the edge of the retina into rows directed towards the centre of the eye and with the double cones arranged parallel in it, all at right angles to the rows. In the mosaic of the *Gadus* and *Merlucius* species, this arrangement is retained quite unchanged even in adult specimens and with only small variations between the species. In *Gaidropsarus, Raniceps* and *Lota*, a regular arrangement of the cones will not be found in adult specimens, but in young ones, distinct rows with regularly arranged twin cones are seen, the pattern being more regular near the edge of the retina than in its central parts. This type of pattern, as well as its variation i exactness between the different regions of the eye, resembles fundamentally that of the Cyprinids described (ENGSTRÖM 1960).

The cone types and the pattern in which they are arranged must thus be regarded as fundamentally very uniform within the family Gadidae. Within the bounds drawn by the genetical equipment, the evolution has followed slightly divergent lines. In the Gadids proper, which are dependent on their eyes for search of food etc., the selection has lead to development of twin cones; in groups in which the power of vision is of less importance, the characters of the visual elements and their organization into distinct patterns may be of little selective value. In such groups, the original pattern is to a varying extent dissolved, and the types are not quite uniform. In the varying pattern of cone types found in

this group, may be seen a relic from the early stage in ehe evolution when their ancestors branched off from the Gadid main stem. Thus, the *Gadus* and *Merlucius* species which have large eyes—presumably meaning that they make use of them—have uniform cone types and strictly arranged cone patterns of the same type. *Gaidropsarus, Raniceps* and *Lota,* on the other hand, all having small eyes —and therefore presumably not being to the same extent dependent on vision— also have cones of slightly aberrant types and a cone pattern, the regularity of which decreases with increasing age.

Summary

Eyes from 10 Gadid fishes have been studied in respect of their cone types and cone arrangement. All species were found to have the same fundamental types of cones, i.e. twin cones and single cones. The ellipsoids of the cones directly touch the external limiting membrane, the myoids surrounding the bases of the cones. The elongated cone nuclei are found inside the membrane except in *Lota,* where they may either penetrate it or may be found totally outside it. In *Gaidropsarus, Raniceps* and *Lota,* the twin cones are consequently not perfect twin cones, the two halves not always corresponding to each other. All the cones (as also the rods) are found to have an elongated "accessory element" of varying shape and of quite unknown function, which is to be found along the outer segment.

The twin cones are arranged in rows in which they are at about right angles to the rows. This pattern has its typical shape in the *Gadus* and *Merlucius* species but is more or less resolved in the other species examined. The differences between the species as regards the cone types and the cone arrangement are considered to be the result of an interaction between the phylogeny and the ecology of the species in question.

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Reproduction in the Female Indian gerbille *Tatera indica cuvierii* (Waterhouse)

by

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(Received May 1961)

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Introduction

The work presented in this paper is part of an investigation into the biology and control of the gerbilles occurring near Bangalore, South India. Earlier studies (PRASAD 1954 a, b and 1956) have dealt with the natural history, food and feeding habits and reproductive cycle of the male gerbille. The gerbilles live in burrows dug deep in the soil on the borders of cultivated fields and do not as a rule get into the villages. MEASROACH (1954) described the changes in the reproductive organs of two species of gerbille occurring in South Africa. *Tatera brantsi* from the Reef area around Johannesburg, Transvaal, breeds all the year round, but at a reduced rate from October to December. *Tatera afra* from the region of south-west Cape breeds from the beginning of August until the end of March. PRASAD (1956) has shown that the male gerbille *Tatera indica cuvierii* is sexually active from July to the end of April and passes through a period of quiescence in May and June. Litters are born from the last week of September to the first week of March. The present paper deals with the reproductive cycle of the female and the analysis of the population structure, so far as it could be determined from a collection made during 1953—54.

Material and Methods

The gerbilles were collected from the fields in the neighbourhood of Bangalore, South India during the period January 1953 to December 1954. The animals were scared out of their burrows and captured by net. A few of the burrow systems were dug out completely during the breeding season and the litters in the nests were collected. Live animals were brought to the laboratory and anaesthetised with ether. The body weight and length were noted. In addition, the following data were regularly taken on the females and classified into different categories following the procedure outlined by DEANESLY and PARKES (1932). Condition of the vaginal orifice; condition of the mammary glands and condition of the nipples were noted. The animals were classified into: Pregnant; Non-pregnant-non-parous; Lactating; non-pregnant-non-parous and immature animals.

The genital tract was removed and fixed in Bouin's fluid. The ovaries and bits of uterus were sectioned and stained with haematoxylin and eosin or with R. A. Groat's tetrachrome stain. In the case of visible pregnancies, the number of embryos and resorbing embryos were counted. The number of corpora lutea in pregnant animals was recorded for later verification with the number obtained by study of the serial sections.

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GROWTH AND BREEDING SEASON

The distribution of pregnancies (Figs. 1, 2) clearly shows that litters are born from the latter part of September through the first week of March. The earliest visible pregnancies were recorded on the 21st September an the latest birth on the 8th March. The first set of young animals born earliest during the breeding season was caught in the open on the 1st November, indicating that weaning possibly ocurred in about 3 to 4 weeks. From November onwards there is a large number of animals of the current breeding season coming up in the catch.

The lightest pregnant female of the breeding season was first caught on 5th December 1953 and weighed 99 grams. It was apparently an animal born during the early part of the same breeding season as could be seen by the low body weight and small size of the animal. The appearance of such pregnancies in animals born during the early part of the current breeding season indicates that females born earliest during a breeding season become sexually mature in the same breeding season of their birth. Hence the period of immaturity in such females is not more than 8 to 9 weeks. PRASAD (1956) showed that the males of the same species showed signs of sexual maturity in about 12 to 14 weeks after birth. From the beginning of December till the middle of February successive young females of the current breeding season become sexually mature depending on the date of their birth.

The distribution of the body weights (Table I) shows that the heavier weight

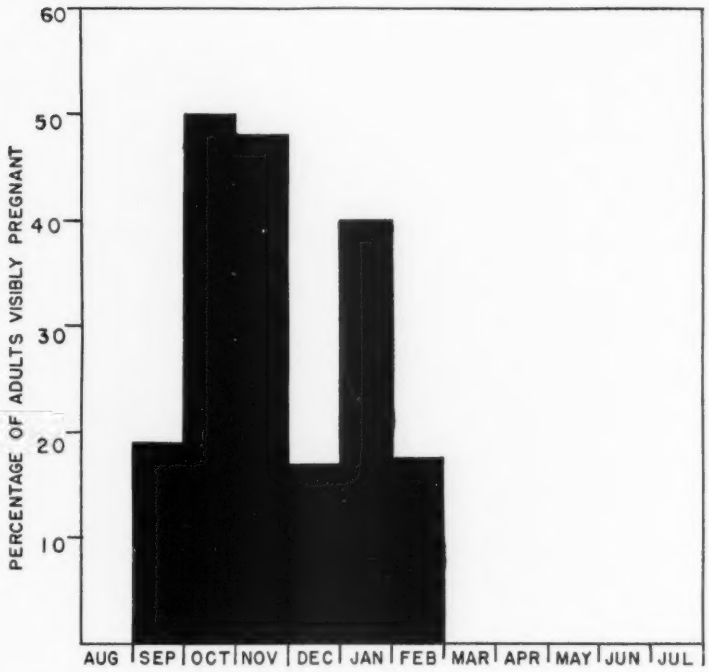

Fig. 1. Diagram showing the percentage of adults visibly pregnant during the different months of the breeding season.

groups with a weight of over 175 grams are found in the middle of the breeding season and continue till the end of the breeding season. There is a gradual reduction in body weights from April to August with the absence of the heavier animals so characteristically seen during the breeding season. This shows that the females born during the previous breeding seasons which had reached heavier body weights during the current breeding season, either suffer heavy mortality or undergo considerable reduction in body weight. The latter appears to be the more probable. There is a general lack of food in the environment from April till the end of June (Prasad 1954 b) and this may be partly responsible for the reduction in weight of the heavier females. The same is true of the males during this period (Prasad 1956). The body weight of the yuong females increases gradually from the middle of the breeding season (December) and by July and August of the subsequent year overlap those of the adults born during the earlier breeding seasons. During this period, April to the end of July, the females are in a state of anestrum. The period of anestrum in the females is much longer than that in the males in which quiescence extends over a short period between May and June. In the first few months of anestrum in the females, April to June, the decreasing body weights of the parous females overlap

Table I. Weight distribution of all the animals collected arranged according to the months.

Weight range grams	Males	Females	Total	% Males	Weight range grams	Males	Females	Total	% Males
January					*June*				
— 50	16	14	30	53.3	— 50	1	0	1	100.0
51—100	13	11	24	54.1	51—100	5	11	16	31.2
101—150	5	3	8	62.5	101—150	17	4	21	80.9
151—200	3	0	3	100.0	151—200	1	0	1	100.0
201—250	1	2	3	50.0	201—250	0	0	0	00.0
Total	38	29	67	56.7	Total	24	15	39	61.6
February					*July*				
— 50	13	8	21	61.9	— 50	0	0	0	00.0
51—100	16	10	26	61.5	51—100	3	10	13	23.3
101—150	4	9	13	30.7	101—150	11	13	24	47.5
151—200	1	2	3	33.3	151—200	1	0	1	100.0
201—250	1	0	1	100.0	201—250	0	0	0	00.0
Total	35	29	64	54.7	Total	15	23	38	39.5
March					*August*				
— 50	13	8	21	61.9	— 50	0	0	0	00.0
51—100	19	23	42	45.2	51—100	2	1	3	66.6
101—150	8	7	15	53.3	101—150	16	27	43	37.1
151—200	0	1	1	00.00	151—200	1	1	2	50.0
201—250	00	0	0	00.00	201—250	0	0	0	00.0
Total	40	39	79	49.9	Total	19	29	48	39.6
April					*September*				
— 50	5	3	8	62.5	— 50	0	0	0	00.0
51—100	8	11	19	42.4	51—100	2	1	3	66.6
101—150	5	7	12	41.7	101—150	16	18	34	48.2
151—200	1	0	1	100.00	151—200	9	2	11	81.9
201—250	0	0	0	00.0	201—250	3	0	3	100.0
Total	19	21	40	47.5	Total	30	21	51	58.8
May					*October*				
— 50	0	0	0	00.0	— 50	10	7	17	58.7
51—100	12	13	25	48.0	51—100	0	0	0	00.0
101—150	7	3	10	70.0	101—150	4	10	14	28.5
151—200	1	0	1	100.0	151—200	6	6	12	50.0
201—250	00	0	0	00.0	201—250	2	0	2	100.0
Total	20	16	36	55.5	Total	22	23	45	50.1

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Table 1. Continued

Weight range grams	Males	Females	Total	% Males	Weight range grams	Males	Females	Total	% Males
November					*December*				
— 50	2	8	10	20.0	— 50	30	18	48	62.4
51—100	0	0	0	00.0	51—100	14	4	18	77.7
101—150	8	10	18	44.4	101—150	3	6	9	33.3
151—200	8	3	11	72.7	151—200	5	1	6	83.3
200—250	1	3	4	25.0	201—250	0	1	1	00.0
Total	19	24	43	44.2	Total	52	30	82	63.4
Grand total for all the months					—	336	297	633	50.3 %

Table II. Visible pregnancies in different months of the breeding season.

Month	Number of females pregnant	Number of embryos visible	Number of corpora lutea	Average number of embryos per female	Average number of corpora lutea per female
January	2	8	8	4.0	4.0
February	3	16	18	5.3	6.0
March	0	0	0	0.0	0.0
April	0	0	0	0.0	0.0
May	0	0	0	0.0	0.0
June	0	0	0	0.0	0.0
July	0	0	0	0.0	0.0
August	0	0	0	0.0	0.0
September	4	26	28	6.5	7.0
October	10	68	72	6.8	7.2
November	9	60	63	6.8	7.0
December	2	13	15	6.5	7.5
Total	30	191	204	6.3	6.8

Comparative figures of visible pregnancies in other species:

Rattus norvegicus	6.1	(Laboratory)
Rattus rattus	7.0	(Wild)
Tatera brantsi	2.64	(Transvaal, South Africa)
Tatera afra	3.98	(South-west Cape, South Africa)

the ascending weights of the non-parous animals of the current breeding season.

In conclusion it may be said that the female gerbilles breed with a regular periodicity, commencing from mid-September to early March, with a period of quiescence from the middle of March to early September.

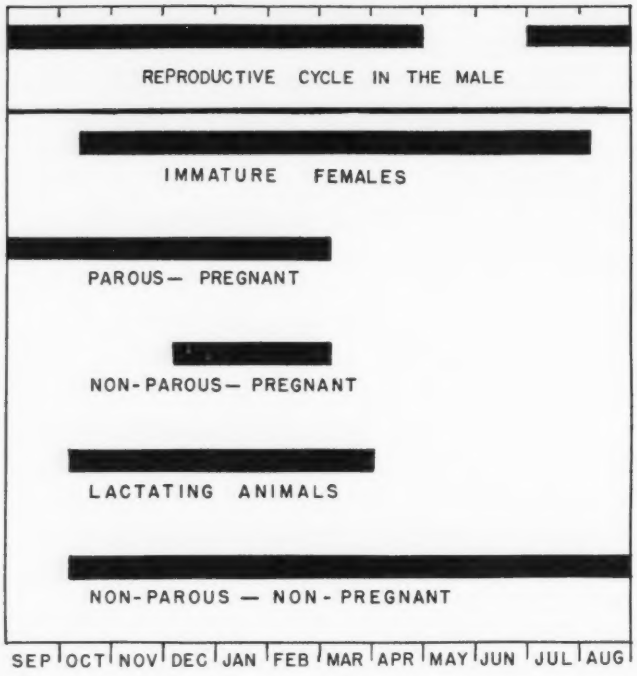

Fig. 2. Composite diagram showing the distribution of the females in different phases of reproductive activity during the year. The duration of reproductive activity of the male is shown at the top for comparison. The female is sexually active from the middle of September to early March and the period of quiescence lasts from the latter half of March to early September.

FERTILITY

Data of 30 pregnancies summarised in Table 2 shows that the average number of healthy embryos included under the category of visible pregnancies is 6.3 (Range 4 to 10). Embryos in-utero month by month, increases gradually from the beginning of the breeding season in September to a maximum in October and November and falls steadily in the latter half of the breeding season. Comparison of the number of corpora lutea with the number of healthy embryos gives an idea of embryonic mortality. The average number of corpora lutea for the 30 pregnant females is 6.8 (Table 2) compared with 6.3 being the number of visible pregnancies. This indicates an intra-uterine mortality of 8 %. As in the case of the laboratory rat, the gerbille experiences post-partum estrus and mates.

The number of embryos per female of different weight groups is given in Table 3. The number of embryos is roughly correlated with the weight of the mother. A similar phenomenon is demonstrated by Perry (1945) in *Rattus norvegicus*.

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Table III. Distribution of pregnancies according to the weight group of the mother.

Number of embryos	Weight group of mother in grams				
	—100	101—150	151—200	201—250	Total
1	0	0	0	0	0
2	0	0	0	0	0
3	0	1	0	0	1
4	0	1	0	0	1
5	2	3	2	0	7
6	0	4	4	0	8
7	0	3	2	1	6
8	0	1	2	2	5
9	0	0	0	1	1
10	0	0	0	1	1
Total	2	13	10	5	30

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Table IV. Number of young in nests compared to embryo rate-visible pregnancies.

Month	Number of nests	Number of young in nest	Average number of young per nest	Embryo rate-visible pregnancies
September	0	0	0	6.5
October	3	22	7.3	6.8
November	2	13	6.5	6.8
December	3	18	6.0	6.5
January	4	19	4.8	4.0
February	2	7	3.5	5.3
March	1	5	5.0	0.0
Total	15	84	5.6	6.3

Comparison of the average number of young in nests (5.6) with the average embryo rate (6.3) for the entire breeding season indicates a neo-natal mortality of 11 %.

AVERAGE NUMBER OF YOUNG IN THE NESTS

The number of young counted in the nests is given in Table 4 according to the months. The nest counts were made in cases where the entire burrow system was dug out and the nest found intact. This gives an average of 5.6 young with a range of 3 to 8 per nest. A review of the figures presented in Table 4 clearly shows that the number of young in the nests is less than the number of embryos in visible pregnancies. The average embryo rate for the entire breeding season is

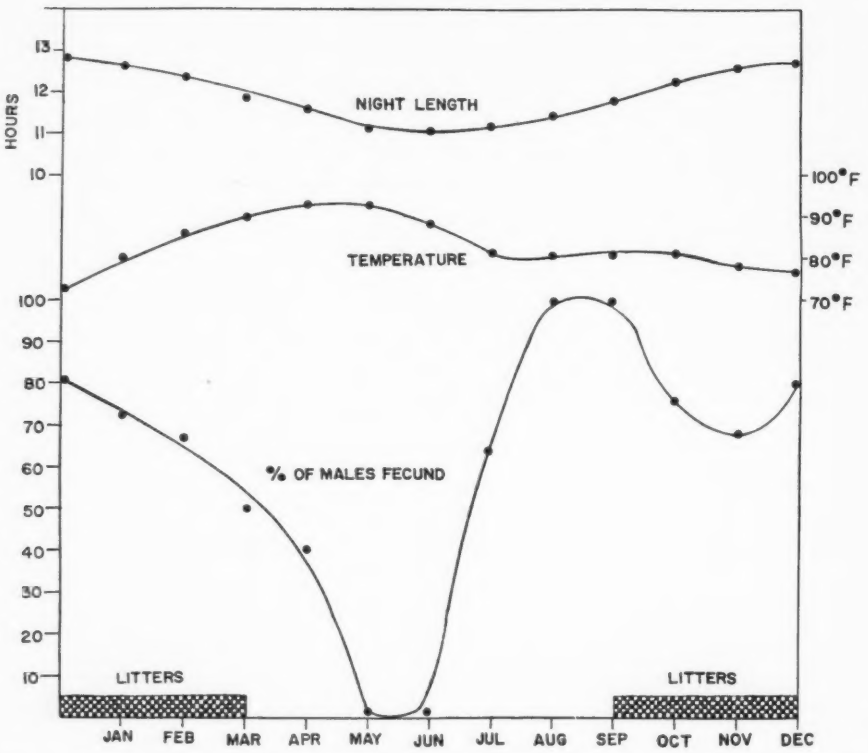

Fig. 3. Composite graph showing the relation of environmental changes with seasonal sexual activity of the male and female gerbilles. The curve at the top shows the variation in the night length in hours. The curve in the middle indicates the variation in air temperature in degrees Fahrenheit. The curve at the bottom shows the monthly percentage of males with spermatozoa in the testes. The shaded portion at the bottom line shows the extent of the breeding season in the females when litters are born.

6.3 as compared with the nest count 5.6. This indicates a neonatal mortality of 11 %. The sexes of the young were not recorded.

ADULT SEX RATIO

Table 1 gives the sex ratios of all the gerbilles collected. The data have been classified according to different weight groups. The percentage of males, 336 out of a collection of 633, is 50.3. For each weight group the percentage is generally more than 50 in favour of the males, except in the weight group 101—150 grams where the ratio of males to females is 47.3. In the heavier weight group 151—250 grams, there is a large preponderance of males, indicating that the males grow to a larger size than the females. Animals were trapped by net after being scared out of their burrows. The presence of fewer females in the heavier weight

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group may indicate that during the breeding season, the heavier females in advanced stages of pregnancy rarely leave their burrows while the males do. The relatively smaller percentage of males in the 101—150 grams group may indicate that the males grow faster and are therefore scarcer in this weight range than the females.

In the gerbille, the percentage of immature males is 57.69 in the weight group below 50 grams. By the time the 101—150 grams group is reached this ratio between males and females levels off to 47.27 %. It is probable that in this group there may be a possibility of weaker males being killed by the larger and stronger males of the same group. It is also possible that cannibalism which is noticed in this species is marked at the time when the young leave the parent burrow to establish their new homes. In their struggle with the larger males or females or stronger animals of the same weight group the smaller and the weaker males of this weight group suffer heavy mortality. Reference has been made to intra-specific struggle of this kind in an earlier paper (Prasad 1954 b).

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RELATION OF MATURITY TO BODY WEIGHT

In a natural population of gerbilles it is rather difficult to determine with accuracy the body weight at which maturity is attained by the females but it is possible within a reasonable limit of probability to estimate the weight taking into consideration the condition of the ovary and occurrence of pregnancies in non-parous animals. As a general routine females with imperforate vagina were classed as immature. The mere fact that the vagina is open is itself no proof of sexual maturity, since Long and Evans (1922) showed that the vagina opens in about 54 % of the female rats some days before the onset of the first estrous and ovulation. My observations on the gerbilles also show that in the majority of the cases where the females were very small in size and weight a perforate vagina was associated with an ovary which did not contain well developed corpora lutea. The presence of corpora lutea can therefore be assumed to be a sign of sexual maturity indicating that the animals have reached a stage when pregnancy can ensue. In the gerbille, no animal with a body weight less than 75 grams and containing corpora lutea was found. Hence all such animals below this weight group which had perforate vagina have been classified as immature. Between the weight range 75 to 100 grams the number of animals with corpora lutea increases indicating that a change from immaturity to maturity occurs in this weight range.

NUMBER OF LITTERS BORNE BY A FEMALE IN ONE BREEDING SEASON

No data are available regarding the length of gestation. The earliest signs of pregnancy are seen in the first week of September when tubal stages of dividing morulae are seen. Advanced pregnancies occur in the latter part of September and

litters are born in the third or fourth week of the same month. Hence the period of gestation may be between 22—24 days. This is similar to the condition in the laboratory rat where gestation lasts 22—23 days. In the south African gerbilles *Tatera brantsi* and *Tatera afra* (MEASROACH 1954) the gestation period is about 22½ days. Post-partum ovulation, mating and delayed implantation of the second set of blastocysts during the lactation of the first litter have been observed. These will be described in greater detail in another paper. Presuming lactation to last about 3 to 4 weeks, as has been shown earlier, an adult female breeding earliest in a breeding season can bear on an average of 3 or 4 litters during a breeding season lasting from September to March. Young females born earliest in the breeding season namely last week of September, become sexually mature and can become pregnant in the last week of December and bring forth the litter in the first or second week of January. Such animals do not have another litter during the same breeding season. This is borne out by the observation that first year females which have borne a litter during their first breeding season do not exhibit post-partum estrus. All the females, regardless of age and weight, go into anestrus at the end of the breeding season in the middle of March. After a protracted period of quiescence lasting from March to August, they become sexually active again in September. The young of a breeding season which have borne one litter in the same breeding season as of their birth become sexually active in early September at the commencement of their second breeding season and bring forth 3 or 4 litters. During a given period in the breeding season, the population of gerbilles contains an admixture of animals in the first, second or third pregnancy and in various phases of lactation and involution.

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Discussion

BREEDING SEASON

Information about the breeding seasons of gerbilles is rather scanty. LATASTE (1887) studied the Algerian gerbille *Dipodillus simme* and the North African gerbille *Pachyuromys duprasi*. Both are polyestrus. He found that gestation usually lasted twenty days and implantation was delayed by suckling. POWELL (1932) stated that the African gerbille *Desmodillus auricularis* has four to six young in a litter; the young breed at three months of age and breeding takes place four times a year. He also reported that *Tatera lobengulae* from the Orange Free State has three to four young in a litter and resembles *Desmodillus* in other features of reproduction. MEASROACH (1954) recorded that the South African gerbille *Tatera brantsi* breeds all the year round; the litter size is 2.9 and five to six litters are born during the year. *Tatera afra* breeds from the beginning of August to the end of March; Litter size is 3.9 and six to seven litters are born

during the breeding season. No information is available concerning the reproduction and breeding seasons of Indian gerbilles except the observation of PHILLIPS (1935) that in the Ceylonese gerbilles the young are born at any time of the year but have generally been noticed during the north-east monsoon, October to April. The number of young is 4.

The female south Indian gerbille *Tatera indica cuvierii* shows a regular cycle of reproductive activity. Breeding season lasts from September to early March and the animals are in a state of quiescence in the intervening period from March to late August. Females born earliest in a breeding season become sexually mature and are pregnant in the last week of December, in the same breeding season as of their birth. Those born after the middle of January to the end of a breeding season do not become sexually mature till the commencement of the next breeding season in September when they are about 6—8 months old. This is shown by the fact that no pregnancies occur between March and September though a large number of adults with heavy body weight are present in the population. The female Indian gerbilles become sexually mature 8 to 9 weeks after birth between the body weight range of 75 to 100 grams. Males of the same species become sexually mature at 12—14 weeks of age (PRASAD 1956). Females of the south African gerbilles become mature at 12 weeks when they weigh 50 grams (MEASROACH 1954).

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ENVIRONMENTAL FACTORS AFFECTING THE BREEDING SEASON

Various environmental factors affecting the breeding season of the male Indian gerbille have been discussed by PRASAD (1956). The data are represented in the form of a composite graph (Fig. 3). None of the environmental factors like light, length of day and night, temperature, rainfall and food is by itself solely responsible for inducing seasonal sexual activity in the male gerbille. In the absence of any environmental factor playing a decisive role in the regulation of sexual cycle in the male, it was suggested that an internal rhythm may be operative with a periodicity of one year, conditioned to some extent by the availability of sufficient amounts of food in the environment. This is also applicable to the regulation of reproductive cycles in the female gerbille.

Summary

The reproductive cycle of the female south Indian gerbille *Tatera indica cuvierii* (Waterhouse) collected from fields near Bangalore, South India is described. The female gerbilles breed with a regular periodicity from September to early March. The period of anestrum or quiescence extends from the middle of March to the end of August or early September. The period of immaturity

is 8 to 9 weeks and the change from immaturity to maturity occurs in the weight range 75—100 grams.

The average number of embryos per adult pregnant female is 6.3. Intra-uterine mortality is 8 % and neo-natal mortality is 11 %.

The adult sex ratio is 50.3 % in favour of the males. Each female brings forth an average of 3 to 4 litters in one breeding season.

It is suggested that an internal rhythm with a periodicity of one year may be responsible for the regulation of seasonal sexual activity in the female gerbille.

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The Development of the Skull in Nerophis *(Lophobranchii)*

by

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(Received May 1961)

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Introduction

The homology of the metapterygoid bone in Syngnathidae is not clearly established and BERG (1947) records the absence of the bone as a distinctive feature of the suborder. JUNGERSEN (1910) also denies the presence of the metapterygoid in the syngnathids. But KINDRED (1924) describing an intermediate stage in the development of the skull of *Syngnathus fuscus* states that the metapterygoid is an intra-membranous ossification without any chondral association. Based on Kindred's observation, DE BEER (1937, p. 515) has posed a question whether the metapterygoid of *Syngnathus* has arisen in the absence of its precursor cartilage. In order to determine the nature of the so-called metapterygoid in Syngnathidae, the development of the skull in *Nerophis* and a comparative study of the skulls

of some of the other members of Syngnathidae was undertaken. In this paper the development of the chondrocranium is described in Part I and in the next, the development of the osteocranium is given with particular reference to some of the bones in the snout region whose homologies are obscure. JUNGERSEN (1910) has given a comparative account of several members of Lophobranchii. GREGORY (1933) has referred to the above paper and figured some skulls but the termonologies of certain bones used by the above authors lack uniformity. The nomenclature of bones used by DE BEER (1937) and the classification as suggested by SMITH (1947) have been adopted in this paper.

Material and Methods

The embryos and a few juvenile specimens of *Nerophis* were obtained through the courtesy of Professor T. PEHRSON of Stockholm by Dr. L. S. Ramaswami who generously lent the material to me. The material was fixed in Zenker's fluid and preserved in 70 % alcohol. Serial sections of different stages were cut 8—10 micra thick and stained in Mallory's triple stain. Some late stages were decalcified in Muller's fluid before sectioning and staining.

Wax model reconstructions of several stages were made and the same have been used for description and illustrations in this paper. Alizarin transparencies of juvenile specimens of *Nerophis,* adult skulls of *Hippocampus guttulatus* Cuv., *Syngnathus serratus* Temm. & Schleg., and *Gastrotoceus biaculeatus* Bloch., have been studied and figured for the sake of comparison.

The following stages have been studied:

Chondrocranium		
Nerophis oequoreus	*Total length*	*Remarks*
Stage 1.	5.0 mm	Wax model
Stage 2.	7.0 "	" "
Stage 3.	8.0 "	" "
Stage 4.	10.0 "	" "
Stage 5.	16.0 "	Transverse sections
Stage 6.	65.0 "	Wax model
Osteocranium		
Stage A.	7.0 "	Transverse sections
Stage B.	8.0 "	" "
Stage C.	10.0 "	" "
Stage D.	16.0 "	" "
Stage E.	65.0 "	Wax model

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Stage F.	82.0 mm	Alizarin transparency
Stage G.	113.0 "	" "
Hippocampus guttulatus	adult	" "
Syngnathus serratus	"	" "
Gastrotoceus biaculeatus	"	" "

PART I

The Development of the Chondrocranium

Stage 1: 5.0 mm total-length embryo. (Figs. 1, 2).

This is the earliest stage studied in which there is no external indication of a snout region characteristic of the late embryos and the adult. The mouth is on the ventral surface of the head as in the majority of teleostean embryos.

The trabeculae (tr) and parachordals (pc) are continuous, the former being situated at a lower level in the floor of the orbital region. The trabeculae join the parachordals in an upward bend in the hypophysial region, enclosing the hypophysial fenestra (hf). In front of the hypophysial fenestra the trabecula communis (tc) is in the form of a spatula broadening in its anterior half. The distal end of the trabecula communis is procartilaginous, lies behind the nasal region and is embedded in a dense mesenchymatous mass of cells which is in close contact with the ectoderm. This mass is the "mesenchymatous plaque" referred to by DE BEER (1931) in *Salmo* and by SRINIVASACHAR (1953) in *Ophicephalus.*

The mesenchymatous mass thins out posteriorly into a median strand and paired lateral strands; the median strand lies in close contact with the ventral surface of the trabecula communis and the paired lateral strands (Fig. 3, mp) which run laterally are continuous with the mesenchyme of the lower jaw at the angle of the mouth.

The parachordals (Figs. 1, 2, pc) flank the notochord (nc) and are separated anteriorly diverging from it. The notochord tapers anteriorly extending unusually upto the anterior extremity of the hypophysial fenestra. The hypophysis lies in the posterior part of the fenestra supported ventrally by the notochord. The parachordals are in procartilaginous state posteriorly where the mesenchymatous occipital processes (oa) are continuous with them. The mesenchymatous occipital processes rise upwards on either side of the dorsolateral surface of the notochord.

The auditory capsule (ac) is chondrifying in the form of a shallow plate with the side walls slightly raised. The anterior basicapsular commissure (abc) is established and is partly procartilaginous.

In the visceral arch skeleton, Meckel's cartilages (mc) are well chondrified horizontal rods converging anteromesially at the symphysial region. The posterior

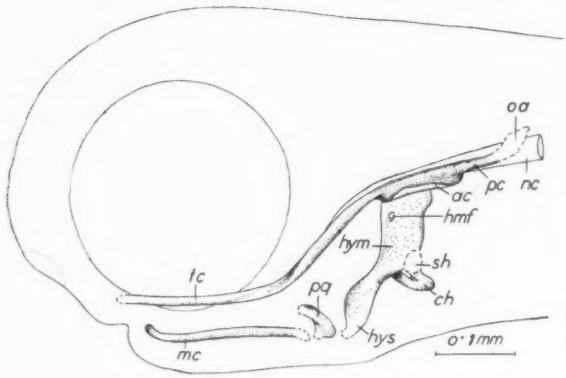

Fig. 1. Lateral aspect of the chondrocranium of *Nerophis* embryo, 5 mm long.

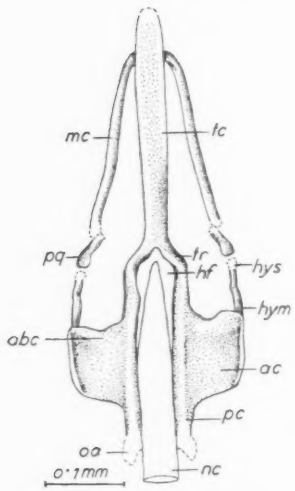

Fig. 2. Dorsal aspect of the chondrocranium of *Nerophis* embryo, 5 mm long.

end of Meckel's cartilage is procartilaginous and immediately behind it, the palatoquadrate (pq) is noticed as a vertical plate with a short anterodorsal process chondrifying in the lateral strand of the "mesenchymatous plaque" as already mentioned. The hyoid arch shows a well developed hyomandibula (hym) articulating with the auditory capsule (ac) dorsally. Ventrally the hyomandibula is continuous with a short symplectic (hys) portion. It is procartilaginous at its anterior end which lies just behind the quadrate (pq). The ramus hyomandibularis facialis passes through a foramen (hmf) situated in the anterodorsal region of the hyobandibular cartilage. The ceratohyal (ch) is well formed and is obliquely placed with its anterior end bearing a small hypohyal. Laterally the ceratohyal is in continuity with an ill-defined rounded stylohyal (sh) which is chondrifying between the ceratohyal and the hyomandibula. The first two branchial arches are represented by two pairs of short cartilaginous horizontal rods.

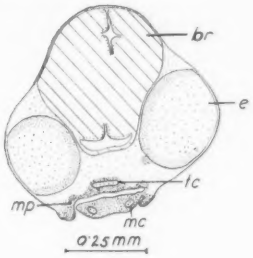

Fig. 3. Transverse section of the embryo of *Nerophis* (5 mm long) in the orbital region.

Stage 2: 7.0—7.5 mm total-length embryo. (Figs. 4, 5).

There has been a rapid growth of the snout and of the cartilages of the chondrocranium. The snout is not straight but has grown vertically backwards so that its distal end with the mouth lies dorsal to the midorbital region.

The prenasal part of the ethmoid plate (ep) is flexed upwards in a backwardly directed oblique curve reaching as far as the middle of the orbit. In the nasal region the ethmoid plate is narrow and rod-like and in front, it broadens into a plate. More anteriorly it again narrows and ends in slight lateral expansions—the preethmoid cornua, which are procartilaginous. A cartilaginous nasal septum has not yet developed. The nasal sacs are separated by a membranous septum which extends between the two parts of the bent ethmoid plate.

In the orbital region the trabecula communis (tc) lies in the midventral region close to the roof of the oral cavity. A membranous interorbital septum extends from the dorsal surface of the trabecula communis to the floor of the cranial cavity. The hypophysial fenestra (hf) is enclosed by the trabeculae and the basal plate. The notochord (nc) projects into the posterior half of the hypophysial fenestra. In front of the anterior basicapsular commissure (abc) a slender mesenchymatous rod of cells extends from the dorsal edge of the hyomandibula to the lateral surface of the parachordal; this is the forerunner of the lateral commissure.

The auditory capsule (ac) has no medial wall. From the lateral wall a pillar-like membranous septum extends to the floor of the auditory capsule forming the septum of the lateral semicircular canal. Septa of the anterior and posterior semicircular canals are represented by short membranous extensions which join the stout septum of the lateral semicircular canal.

The occipital processes (oa) are cartilaginous and have fused with the posteromedial wall of the auditory capsule enclosing a foramen, the fissura metotica (Fig. 4, fme) for the exit of the glossopharyngeal and the vagus nerves. This foramen is in the form of a short canal as in *Gasterosteus* (SWINNERTON, 1902) and *Syngnathus* (KINDRED, 1921). In *Hippocampus* (KADAM, 1958) the metotic foramen lies in the floor of the basal plate. The occipital processes in *Nerophis* project posteriorly for a short distance forming a lateral wall to the foramen magnum.

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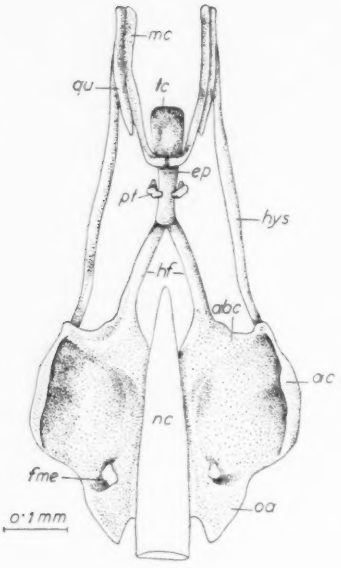

Fig. 4. Dorsal aspect of the chondrocranium of *Nerophis* embryo, 7.5 mm long.

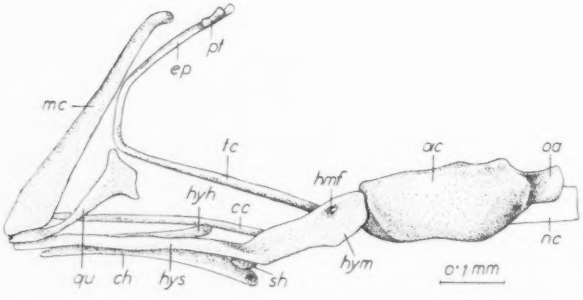

Fig. 5. Lateral aspect of the chondrocranium of *Nerophis* embryo, 7.5 mm long.

The pterygoid processes of the quadrate (pt) have chondrified independently and lie close to the distal part of the ethmoid plate. The anterior ends of the processes are broader and their medial ends are connected with each other by means of a mesenchymatous mass which is in close contact with the procartilaginous preethmoid cornua. The mesenchymatous mass corresponds to the "intermediating body" described by HOLMGREN (1943) in teleosts. The quadrate gives articulation to Meckel's cartilage anteriorly by its cylindrical part and posterodorsally it consists of a vertical plate of cartilage.

Meckel's cartilages (mc) which were horizontal in the earlier stage are vertical and tilted backwards in the present stage so that their symphysis lies dorsally in the midorbital region. The hyosymplectic cartilage is very much elongated with an anterior horizontal symplectic portion (hys) and a vertical plate-like hyomandibular portion (hym). The distal part of the symplectic reaches the

anterior limit of the quadrate. The anterior ends of the hypophyal (hyh) and ceratohyal (ch) of each side are fused for a short distance and posteriorly they are separate as distinct rods, the former being connected to the copula communis (cc) and the latter to the hyomandibula through a small distinct stylohyal (sh).

The hyomandibula articulates dorsally with the anterolateral surface of the auditory capsule. The articulation is far anterior when compared with the usual teleostean condition. The dorsoposterior end of the hyomandibula appears to have fused with the auditory capsule in some specimens of the same age.

The first four branchial arches are present as paired cartilaginous rods. The medial ends of the first arch are attached to the posterior end of the copula communis. The remaining branchial arches meet ventromedially as there are no basibranchs.

Stage 3: 8.0 mm total-length embryo. (Fig. 6).

The chondrocranium is almost similar to that of the previous stage. The bend of the ethmoid plate is in the process of being straightened. As a result of this process, the anterior bent part of the ethmoid plate is lesser in extent than the posterior straightened part. The pre-ethmoid cornua are broader providing articulation to the pterygoid processes (pt) of the quadrate.

The mesenchymatous mass in front of the anterior basicapsular commissure observed in the previous stage is converted in the present stage into a young cartilaginous lateral commissure. Laterally the commissure is continuous with the base of the short postorbital process (pop) which has grown up from the anterolateral corner of the auditory capsule (ac). The medial edge of the auditory capsule has grown a little higher than in the previous stage and there is greater fusion of the occipital processes with the posterior wall of the auditory capsule.

In the mandibular arch, Meckel's cartilages (mc) are almost vertical due to the straightening of the ethmoid plate and shifting of the mouth from the mid-orbital region to the front of the orbit. The pterygoid process of the quadrate lies vertically on either side of and articulating with the lateral surface of the preethmoid cornu. The "intermediating body" of mesenchymatous tissue between the medial ends of the pterygoid processes noticed in the earlier stage has disappeared. Whether it has fused with the preethmoid cornua, as discussed by Holmgren (1943) in fishes generally, could not be found out in my slides. However, the distal end of the ethmoid plate is broader and thicker than in the previous stage.

A mesenchymatous condensation has appeared in front of the anterior end of the ethmoid plate. It is the rudiment of the rostral cartilage.

The anterior end of the hyosymplectic (hys) lies below the quadrate (qu) as before but slightly posteriorly to the tip of the quadrate.

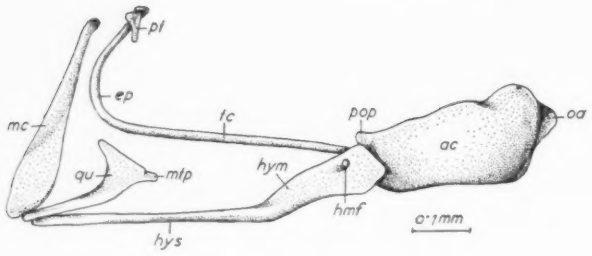

Fig. 6. Lateral aspect of the chondrocranium of *Nerophis* embryo, 8 mm long.

Stage 4: 10.0 mm total-length embryo.

The snout is straightened out completely resulting in the corresponding straightening of the ethmoid plate. The ethmoid plate gently slopes upwards anteriorly as the gape of the mouth faces upwards. The preethmoid cornua are broader and the pterygoid processes articulate with their ventrolateral surfaces. An internasal septum is still membranous and there is no other cartilage in the nasal region other than the ethmoid plate.

The anterior half of the hypophysial fenestra lodges the eye-muscles forming the posterior "myodome" which has been described as fenestra myodomus ventralis by KINDRED (1921) in *Syngnathus* and KADAM (1958) in *Hippocampus*. The posterior region of the hypophysial fenestra has axially the anterior tip of the notochord extending into it. The hypophysis is situated in this region dorsally to the notochord. Behind the hypophysial fenestra the notochord separates the medial edges of the parachordals throughout as in the 12 mm stage of *Syngnathus* (KINDRED, 1921). In a 9 mm embryo of *Hippocampus* (KADAM, 1958) the basal plate is connected by a prootic bridge behind the hypophysial fenestra and the notochord lies in the posterior region of the basal plate.

The postorbital process of the auditory capsule has grown further dorsally into the lateral wall behind the orbit. The lateral commissure though slender is complete forming the anterior limit to the facialis foramen. The lateral walls of the auditory capsules have extended dorsally in the middle region but they do not meet to form any roofing cartilage.

Meckel's cartilages are directed obliquely forwards due to the straightening of the snout and the ethmoid plate. Lateral to the symphysial region of Meckel's cartilages there is a pair of dense masses of fibrous tissue representing the infralabial cartilages.

The rostral cartilage has chondrified in the mesenchymatous condensation in front of the preethmoid cornua.

The hyomandibula has acquired a greater extent of articulation with the ventrolateral surface of the anterior region of the auditory capsule.

Stage 5: 16.0 mm total-length embryo.

The chief interset in this stage is the development of an independent nasal septum extending on the middorsal region of the ethmoid plate with the perichondria of the two remaining distinct. In the posterior region of the nasal sacs the ventral border of the nasal septum is expanded over the ethmoid plate and the lateral edge is continuous with a vertical rod of cartilage, the lamina orbitonasalis (ectethmoid cartilage) which is fused dorsally with the thickened edge of the nasal septum. The nasal region at this stage resembles in its development and composition that of the 9 mm stage of *Hippocampus* (KADAM, 1958). Behind the lamina orbitonasalis the nasal septum is continued by a membranous interorbital septum. The thickened dorsal edge of the nasal septum however, extends back into the roof of the orbital region for a short distance before bifurcating into two short diverging orbital cartilages.

The trabecula communis which is continuous with the parachordals in the previous stages has broken down in the middle of the orbit. This type of a discontinuity is common in teleosts and occurs at various stages of development in different forms.

A small cartilaginous rod has appeared in the roof of the posterior region of the orbit where the postorbital processes have grown further dorsally. If this median piece of cartilage were continuous with the postorbital processes, a tectum transversum would have been present.

The stout membranous septum of the lateral semicircular canal has chondrified and is the only cartilaginous septum in the auditory capsule. In the posterior region, the occipital processes have fused dorsally to the foramen magnum forming a short tectum posterius.

The basal plate behind the hypophysial fenestra is continuous since the notochord has receded to the posterior region where it still separates the medial borders of the basal plate.

A little posterior to the base of the septum of the lateral semicircular canal, resorption of the cartilage in the floor of the capsular wall has resulted in the formation of the basicapsular fenestra which is covered by a membrane. A minute opening in a similar position has been described in *Syngnathus* (KINDRED, 1921) and *Hippocampus* (KADAM, 1958). In the latter fish the foramen enlarges and becomes confluent with the metotic foramen. The fenestra is fairly large in *Gasterosteus* (SWINNERTON, 1902).

The anterior end of the hyosymplectic cartilage has receded further and now is seen below the posterior border of the quadrate cartilage.

Stage 6: 65.0 mm total-length young fish. (Figs. 7, 8).

Though the gap is very great between the previous stage and this one, no new development of cartilage has occurred as most of the cartilages have already

appeared in the preceeding stage. There has been a general growth of the chondrocranium and ossifications in some regions have set in.

The ethmoid region: The prenasal part of the ethmoid plate (ep) is cylindrical with broadened distal part bearing the preethmoid cornua (ec). In front of the nasal region the ethmoid plate is broader and exhibits a dorsal ridge. The ridge increases in height anteroposteriorly in the nasal region forming a well developed nasal septum (ns) which is indistinguishably fused with the ethmoid plate below, obliterating the indication of its independent origin in the early stages. The postnasal walls are formed by short laminae orbitonasales (lon) which are fused with the massive posterodorsal edge of the nasal septum. A foramen olfactorium advehens is enclosed between the lamina orbitonasalis and the nasal septum. There is no sphenoseptal commissure.

The orbito-temporal region: The trabecula communis (tc) is noticed as a short pointed projection from the ethmoid plate in the anterior region of the orbit. The posterodorsal edge of the nasal septum extends upwards and backwards in the roof between the two orbits. In the middle region of the orbit it gives off a pair of short orbital cartilages (orc). The interorbital septum is membranous and is attached below to the parasphenoid throughout its length except behind the nasal region where it is attached to the short trabecula communis (tc). The septum gradually decreases in its height posteriorly and ends in the region of the posterior "myodome". As in *Hippocampus* (KADAM, 1958) the "myodome" is deep, the floor being formed by the parasphenoid and the side wall partly by the wing-like extension of the parasphenoid and partly by the mesial edge of the pila lateralis (pl) which has developed in front of the lateral commissure (lc) enclosing the trigeminal foramen (tf). The lateral wall in the posterior part of the orbit is formed by the postorbital process (pop).

In the roof of the postorbital region the small cartilage observed in the previous stage has grown into a triangular plate. The broad anterior part of the plate is thin and represents the tectum transversum (Fig. 7, ttr); the posterior part is narrow and cylindrical corresponding to the taenia tecti medialis (tm) as in *Hippocampus* (KADAM, 1958).

The auditory region: As in other syngnathids the auditory capsule does not show any external indications of the semicircular canals as they are short and broad. The capsular walls have extended dorsally over the cranial cavity in the posterior part of the chondrocranium. However, they do not meet medially and therefore a tectum synoticum is absent. But I have been able to notice a cartilaginous tectum synoticum (See Fig. 12, tsy) in the posterior region of the auditory capsule in an adolescent specimen (113 mm total-length). Remnants of a similar tectum has also been observed in the cross sections of an adult *Syngnathus serratus* (See Fig. 14, tsy). KINDRED (1921) described a tectum synoticum in the anterior region of the auditory capsule in *Syngnathus fuscus* which I am unable to find in *Serratus*.

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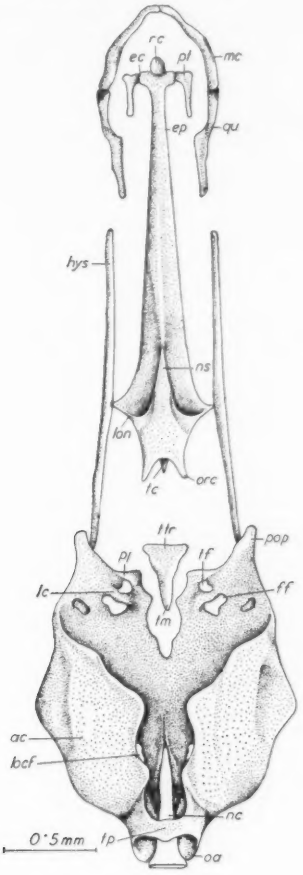

Fig. 7. Dorsal aspect of the chondrocranium of *Nerophis* young, 65 mm long.

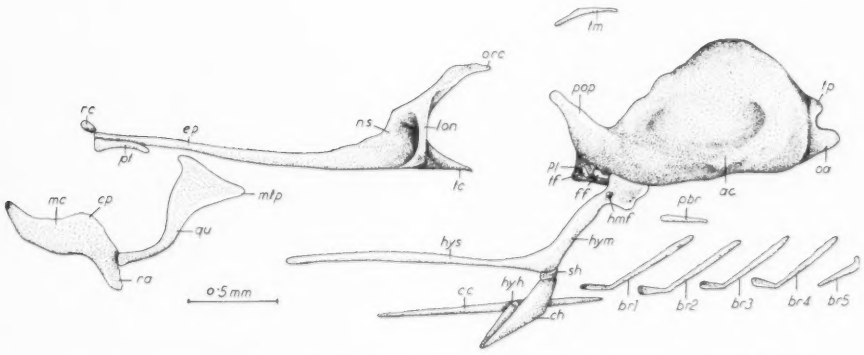

Fig. 8. Lateral aspect of the chondrocranium of *Nerophis* young, 65 mm long.

The basicapsular fenestra (bcf) is larger than it was in the previous stage and is covered by a bony lamella which is continuous with the perichondrium of the cartilage forming the lateral border of the fenestra. Another fenestra has appeared by the resorption of the cartilage in the anterolateral wall of the auditory capsule at the region of articulation of the hyomandibula. The head of the hyomandibula could be seen partially in the dorsal view through the foramen posterodorsal to the lateral commissure (Fig. 7,1c). In *Hippocampus* (KADAM, 1958), a spheno-pterotic ridge overhangs the region of articulation of the hyomandibula with the auditory capsule. Such a ridge is not seen in *Syngnathus* (KINDRED, 1921) or in *Nerophis*.

The occipital region: The occipital processes (oa) form a slender arch over the foramen magnum. The base of the arch projects posteriorly for a short distance on either side of the notochord. Due to the greater fusion of the occipital arch with the posterior wall of the auditory capsule the foramen for the glossopharyngeal and the vagus nerves lies more laterally on the posterior face of the auditory capsule.

The basal plate and notochord: The notochord (nc) lies in the posterior region of the basal plate separating the posterior parts of the parachordals. The anterior tip of the notochord is very narrow and lies on the cerebral surface in between the mesial edges of the parachordals. In front of the anterior tip of the notochord the parachordals meet medially for a short distance and are fused further anteriorly.

The visceral arch skeleton: The pterygoid process (pt) anteromesially articulates with the lower surface of the preethmoid corn of the ethmoid plate exhibiting the rostropalatine articulation or the "acrartete" type of SWINNERTON (1902). At no stage is the pterygoid process continuous with the main body of the palatoquadrate as in the majority of the siluroids except *Arius* (SRINIVASACHAR, 1959).

The quadrate cartilage (qu) is for a greater part invested by perichondral bone. Anteroventrally the quadrate articulates with the cartilage of the lower jaw by a broad surface. Behind the articular region the cartilage is narrow and posteriorly it rises up as a broad thin sagittal plate. The anterodorsal corner of the sagittal plate shows a small process towards the posterior end of the pterygoid process of the quadrate. Posterodorsally also there is a process which may correspond to the metapterygoid process of *Syngnathus* (KINDRED, 1921) and *Hippocampus* (KADAM, 1958).

Meckel's cartilages (mc) are obliquely placed with an anterodorsal symphysis. Each Meckel's cartilage is enclosed by the dentary bone. The main shaft of the cartilage posteriorly shows a small coronoid process (cp) in front of the articular region and a short vertical retroarticular process (ra) extends downwards posteriorly to it.

On either side of the symphysial region there is a thick fibrocartilaginous mass

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representing the infralabial cartilage also seen in *Syngnathus* and *Hippocampus*.

A well developed rostral cartilage (rc) lies in front of and above the distal end of the ethmoid plate. The cartilage is bound posteriorly by a pair of fibrous tissue strands to the anterior ends of the pterygoid processes of the quadrate.

The anterior end of the symplectic part of the hyosymplectic cartilage (hys) lies farther behind the quadrate cartilage and does not come in contact with it as it did in the previous stages. The hyomandibula (hym) is stouter, obliquely vertical and is continuous with the symplectic. Dorsally the hyomandibula gradually becomes a thin plate and is constricted in the region of the foramen for the hyomandibularis branch of the facial nerve (hmf), due to the development of the bone. The hyomandibular cartilage articulates with the ventrolateral surface of the auditory capsule extending from the base of the postorbital process to the region of the anterior semicircular canal.

The stylohyal (sh) is a rectangular piece of cartilage intercalated between the hyomandibula and the ceratohyal (ch). The hypohyal (hyh) and the ceratohyal cartilages of each side are fused at their anterior ends; the posterior end of the hypohyal lies against the copula communis (cc). The ceratohyal as stated above articulates posteriorly with the stylohyal.

The ventromedial ends of the first arch (brl) lie above the posterior end of the copula communis. Only one pair of pharyngobranchs (pbr) is present. In the second, third and fourth branchial arches the inner ends meet ventrally and there are no basibranchs. However, behind the symphysis, in the second branchial arch there is a minute cartilaginous rod seen only in a few sections. The fifth arch has appeared and consists of two ceratobranchs whose anteroventral ends are widely separate and do not meet medially.

Sclerotic cartilages are present throughout as ring-like cartilages, one in each optic vesicle occupying the greatest circumference of the eye ball.

DISCUSSION

In the earliest stage of *Nerophis oequoreus* described in this paper, it is observed that the trabecula communis is long and its anterior end is procartilaginous embedded in a dense mesenchymatous mass of cells which is in close contact with the ectoderm. The trabecula in this region is chondrifying as a single structure. As NORMAN (1926, p. 414) pointed out it is possible that the trabecula communis has arisen as a single structure. The unusual extension of the anterior end of the notochord so as to reach almost the apex of the hypophysial fenestra may also signify that the trabecula communis has arisen as a single structure.

The ethmoid region of Syngnathidae is a highly specialised part of the chondrocranium. It forms the long axial structure of the snout. In early stages the prenasal part of the ethmoid plate is bent upwards in *Hippocampus* (RYDER, 1881) and *Syngnathus* (KINDRED, 1921). KADAM (1958), further described a

backward bend of the ethmoid plate in a 9 mm. embryo of *Hippocampus*. In *Nerophis* also the ethmoid plate is bent upwards and backwards in the 7 mm. stage. This is a curious feature in the syngnathids and it is difficult to explain this phenomenon of the bent vertical growth and its subsequent straightening. The hyosymplectic cartilage which is equally elongated contributing to the elongation of the snout does not show any bending. It is likely that this peculiar bend noticed in three genera of Syngnathidae examined may have some phylogenetic significance, which at present, I am unable to comment upon.

The nasal capsules of Syngnathidae exhibit an extraordinary condition regarding their development. Generally in teleosts the nasal septum arises as a median outgrowth on the dorsal surface of the ethmoid plate and the laminae orbitonasales grow up as vertical pillars from the lateral edges of the ethmoid plate. In *Nerophis* as in *Hippocampus* (KADAM, 1958) the nasal septum and the laminae orbitonasales arise together independently of the ethmoid plate late in ontogeny. Yet another condition is noticed in *Syngnathus* (KINDRED, 1921) and *Siphonostoma* (NORMAN, 1926). In *Syngnathus* the laminae orbitonasales (ectethmoid cartilages of KINDRED) appear first as independent rods of cartilage and later fuse to form a nasal septum. In *Siphonostoma* the nasal septum (mesethmoid cartilage of Norman) and the ectethmoid cartilages arise independently of each other and remain so even in a late stage. Among other teleosts, in *Cyclopterus* (UHLMANN, 1921) the ectethmoid cartilages arise independently of the ethmoid plate. According to HOLMGREN (1943), in the blastemal condition the lamina orbitonasalis is always independent of the ethmoid plate but fuses with it early forming the hind wall of the nasal capsule. In the syngnathids so far studied the laminae orbitonasales are always independent of the ethmoid plate and along with the nasal septum fuse with the plate later. JARVIK (1954) considering the independent origin of the lamina orbitonasalis suggests that the lamina represents the suprapharyngeal element of the premandibular arch.

The lateral commissure in *Salmo* and in other teleosts (DE BEER, 1937) is formed by the fusion of two processes viz., the postpalatine process and the prootic process. In *Ophicephalus* (SRINIVASACHAR, 1953) the two processes are developed but are unconnected to form a lateral commissure in a late stage (24 mm. long embryo). However, SWARUP (1953) states that the two processes unite to form a lateral commissure in *O. punctatus* (7.5 mm. stage). In *Gasterosteus* (SWINNERTON, 1902) only the prootic process is fused with the lateral edge of the parachordal forming a lateral commissure. In *Nerophis* the lateral commissure arises as a single slender rod of cartilage stretching in front of the facial nerve. The lateral edge of the lateral commissure rests upon the dorsal edge of the hyomandibula but its fusion with the base of the postorbital process of the auditory capsule takes place quite early. The independent origin of the lateral commissure in *Nerophis* supports the conclusion of HOLMGREN (1943) and of JARVIK (1954) that the lateral commissure arises from a separate rudiment proved to be visceral

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in origin by them and therefore, the latter author compared the lateral commissure of teleosts with the suprapharyngeal of *Eusthenopteron.*

The auditory capsules of *Syngnathus* (KINDRED, 1921) and *Hippocampus* (KADAM, 1958) do not show any cartilaginous septa of the semicircular canals. They are merely represented by ridges on the inner surface of the capsular wall. In the early stages of *Nerophis* the septa are membranous and complete though short and slender except that of the lateral semicircular canal which is stout. This septum in later stages chondrifies and is the only septum in the fully developed capsule. The other two septa which are membranous in early stages disappear later. KINDRED (1921, 1924) does not record any septum in *Syngnathus* but in my serial sections of the adult skull of *Syngnathus serratus* a short bony septum of the lateral semicircular canal is noticed.

The roof of the chondrocranium in *Nerophis* shows only a small triangular isolated piece of cartilage lying in the anterior part of the auditory region as in *Hippocampus* (KADAM, 1958). Further, *Nerophis* resembles *Hippocampus* in possessing a short tectum posterius. Though a tectum synoticum is absent in the early and advanced stages of *Nerophis* and *Syngnathus,* the 113 mm. young specimen of the former and the adult of the latter exhibit a short tectum synoticum in the posterior region of the auditory capsule inside the supraoccipital bone.

The processus pterygoideus develops independently of the quadrate and remains separate troughout in *Nerophis.* In *Hippocampus* and *Syngnathus* also the process is independent but is connected with the quadrate by a ligamnetous tissue. In earlier stages of *Nerophis* the anterior ends of the pterygoid processes are connected by a mesenchymatous body which in later stages has either fused with the preethmoid cornua or has disappeared. Holmgren calls this body the "intermediating body" and states that it may chondrify giving rise to a palatoquadrate commissure. This commissure has not been observed by me in *Nerophis.* From the beginning, the pterygoid process articulates by means of a rostro-palatine process with the preethmoid cornu of the ethmoid plate. There is no ethmo-palatine articulation.

The branchial skeleton of *Nerophis* agrees with other syngnathids in the reduction of several elements. The ceratohyal and hypohyal are separate and distinct in *Hippocampus* and *Syngnathus* while in *Nerophis* the two cartilages of each side are united distally for a short distance. JUNGERSEN (1910) described a pharyngobranch in the second arch in the adult skull of *Nerophis.* In the chondrocranium, however, I have not been able to notice any indication of the single pharyngobranch to associate it with the second arch. There are no basibranchs in any of the arches except the first where the posterior end of the copula communis extends ventrally as in *Hippocampus* and *Syngnathus.* In the second arch a minute basibranch is present in the 65 mm. stage of *Nerophis* while in *Syngnathus* and *Hippocampus,* there is no basibranch in the second branchial arch. In *Syng-*

nathus the third and fourth basibranchs which are present in the 12 mm. stage are absent in a 43 mm. specimen (KINDRED, 1924).

From a comparative study of the chondrocrania of *Syngnathus, Hippocampus* and *Nerophis,* some striking features of the syngnathid chondrocranium are noticed which are as follows:

1. The prenasal part of the ethmoid plate is highly elongated and bent in early stages. The distal end of the ethmoid plate is broadened to form the preethmoid cornua,
2. the nasal septum and the laminae orbitonasales arise independently of the ethmoid plate during development and fuse later,
3. the dorsal edge of the nasal septum is broad and extends posteriorly into the orbit bifurcating into short orbital cartilages,
4. the postorbital processes of the auditory capsules are not connected with the orbital cartilages,
5. the roofing cartilages are reduced, there being a short tectum posterius,
6. the cartaliginous septa in the auditory capsules are reduced or are absent and a basicapsular fenestra develops in late stages by resorption of cartilage,
7. a lateral commissure and a pila lateralis are present,
8. Meckel's cartilages are vertical or oblique in early stages and later become horizontal when the straightening of the ethmoid plate takes place,
9. the hyosymplectic is very much elongated carrying with it the quadrate and Meckel's cartilages to the anterior end of the snout,
10. the pterygoid process of the quadrate remains independent of the quadrate and may be connected with it by connective tissue or ligament; there is only a rostro-palatine articulation,
11. the infralabial cartilages are present in a rudimentary condition,
12. a well developed rostral cartilage is present,
13. the branchial arches do not possess their full complement, and
14. the sclerotic cartilages are present in the optic cups.

PART II

The Development of the Osteocranium

The ossifications have been described in the stages employed for the description of the chondrocranium as well as in two more advanced stages. Ontogenetically the bones have been classified into membrane bones, cartilage bones, and chondromembranal bones as done by SMITH (1947).

No ossification is seen in the earliest stage studied (5.0 mm. total-length embryo).

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Stage A: 7.5 mm. total-length embryo.

In stage 2 of the chondrocranium described in part I of this paper, some of the ossifications have already appeared in the form of minute spicules. The membrane bones that have developed in this stage are the premaxillae, the maxillae, the dentaries, the angulars and the parasphenoid. The quadrate though phylogenetically a cartilage bone, has a large intramembranous ossification fused with a small perichondral portion of the quadrate cartilage. Hence, ontogenetically the quadrate is a chondromembranal bone.

The premaxillae are very small lying in front of the larger maxillae in the dorsal surface of the upturned snout region behind the mouth. The premaxillae and the maxillae are medially in contact with a condensed mesenchymatous mass, the anlage of the rostral cartilage.

The dentaries flank the upper half of the vertical Meckel's cartilages. Each dentary anteriorly has invaded the perichondrium of Meckel's cartilage a little behind the symphysial region.

The angular has ossified intramembranously on the lateral aspect of the lower half of Meckel's cartilage. The dorsal border of the angular is overlapped by the dentary.

The parasphenoid extends beneath the trabecula communis from the midorbital region to the anterior part of the basal plate. In the posterior region of the hypophysial fenestra the bone expands laterally forming a complete floor beneath the distal end of the notochord. Posteriorly the parasphenoid forks, each limb lying on the ventrolateral aspect of the stout notochord. In this region the parasphenoid may have paired centres of ossification but I have not observed separate centres.

The quadrate as already mentioned is a chondromembranal bone possessing a long limb of intramembranous ossification which lies on the dorsal aspect of the symplectic cartilage. Anteriorly this limb embraces and slightly extends into the perichondrium of the posteroventral border of the quadrate cartilage. While the intramembranous part is well ossified the perichondral part appears to be an extension of the intramembranous part. Probably the cartilage in the region of the intramembranous ossification has been suppressed during phylogeny.

Stage B: 8.0 mm. total-length embryo.

A new membrane bone that has appeared in this stage is the ectopterygoid which extends from the posterior end of the pterygoid process of the quadrate to the anterior face of the quadrate cartilage. The ectopterygoid is more or less vertical and appears to have ossified in the ligament that stretches in the earlier stage between the pterygoid process and the quadrate.

The parasphenoid has grown below the ethmoid plate.

Stage C: 10.0 mm. total-length embryo.

The vomer has developed in this stage as a small spicule in the mesenchymatous condensation below the anterior part of the prenasal part of the ethmoid plate.

The perichondral ossification of the quadrate which is continuous behind with the intramembranous part has extended anteriorly towards the articular region. It is also seen to be spreading upwards on the outer and inner perichondria of the vertical plate of the quadrate. The intramembranous part has extended posteriorly upto the posterior region of the orbit.

Stage D: 16.0 mm. total-length embryo.

The premaxillae and the maxillae have grown further and articulate with the rostral cartilage medially. The vomer has extended anteriorly beneath the broadened distal end of the ethmoid plate. Posteriorly it lies beneath the parasphenoid which has grown forwards below the ethmoid plate in front of the nasal region.

The frontals develop in the membrane extending posteriorly from the lateral surface of the posterodorsal margin of the nasal septum to the posterior region of the orbit. They are separated in the middle by a membranous strip.

The supraoccipital, like the quadrate, ossifies largely as an intramembranous ossification behind the frontals and separating them. Only a very small anterior part of the bone is perichondral surrounding the posterior part of the taenia tecti medialis. In the stage the supraoccipital bone does not quite reach the occipital region of the skull.

The entopterygoid has appeared as a tiny intramembranous ossification mesial to the dorsal edge of the vertical plate of the quadrate cartilage. The ectopterygoid has developed an anterior limb extending beneath the horizontal cartilaginous pterygoid process of the quadrate.

The intramembranous part of the quadrate bone has enlarged enclosing the anterior half of the hyosymplectic cartilage in a deep groove open mesially. Posteriorly the quadrate is narrow and ends between the symplectic and the preopercle which has ossified in the membrane lateral to the symplectic and ventral half of the hyomandibular cartilage.

The symplectic is a chondromembranal bone with the perichondral part in the anterior region of the hyosymplectic cartilage co-ossifying with the intramembranous part which rises up from the perichondral part in the lateral wall of the oral cavity at the level of the nasal region of the skull.

The ethmoid bone is made up of a large intramembranous ossification on the middorsal surface of the ethmoid cartilage in front of the nasal region. It covers almost the posterior half of this cartilage but nowhere is connected with it. Only in the nasal region where the cartilaginous nasal septum is developing, the ossifi-

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cation appears to be continuous with the perichondrium of the anterior part of the nasal septum. Here again as in the case of the quadrate and the supraoccipital the intramembranous part of the ossification is far greater than the perichondral part.

As Meckel's cartilages have changed their bearing (see chondrocranium), the dentaries lie in front of the angulars and not above them as they did in the earlier stage. The angulars posteriorly have fused with the lateral perichondrium of Meckel's cartilage in front of the articular region.

Of the opercular series, the preoparcle and the opercle have made their appearance. The preopercle has ossified ventrolaterally to the posterior part of the quadrate and laterally to the symplectic. The preoparcle starts anteriorly as a narrow thin plate and gradually spreads out covering the symplectic and the lateral aspect of the lower half of the hyomandibular cartilage.

The opercle is ossifying in the lateral wall of the branchial chamber behind the hyomandibula.

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Stage E: 65.0 mm. total-length young fish. (Fig. 9).

The frontals (fr) overlap each other mesially and form a roof extending from the nasal region to the anterior region of the auditory capsules. Posterolaterally the frontals have grown down forming the posterior border to the orbits and they cover the dorsolateral surface of the cartilaginous postorbital process. In this region the frontal is suturally connected with the dorsal margin of the sphenotic bone (sph). Posteriorly the frontals overlap the anterolateral borders of the supraoccipital and anteriorly the posterior end of the ethmoid bone.

The vomer (vo) is broad and flat distally below the preethmoid cornu region. Posteriorly to this region the vomer is V-shaped in cross section and the ethmoid cartilage is lodged in the gutter between the two limbs of the vomer. Further posteriorly the vomer is in the form of a thin pointed shaft lying in a groove on the midventral surface of the ethmoid plate.

The parasphenoid (psp) has prominent wing-like lateral ascending processes in the posterior "myodome" region. These lateral processes come in contact with the ventral edge of the pila lateralis. Behind the hypophysial fenestra the parasphenoid becomes narrow and lies beneath the basal plate in the midventral region extending upto the occipital region.

The ectopterygoid (ect) has extended ventrolaterally to the pterygoid process upto its anterior region. The entopterygoid (ent) forms a cap over the dorsal edge of the quadrate and posteriorly it continues as a long bony shaft.

The premaxillae (pmx) and the maxillae (mx) have dorsomedial limbs articulating with the rostral cartilage (rc). Each maxilla articulates with the cartilaginous maxillary process of the pterygoid process of the quadrate.

The dentary (den) has anteriorly a canal and posteriorly a groove on the inner

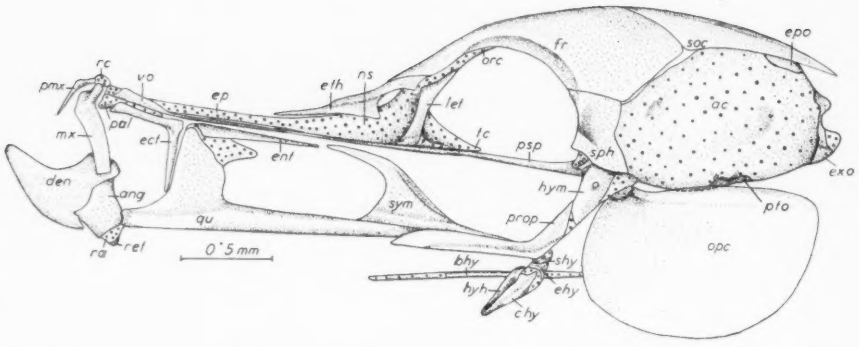

Fig. 9. Lateral aspect of the developing osteocranium of *Nerophis* young, 65 mm long. Cartilage shown by large dots.

surface for Meckel's cartilage. The angular (ang) has extended and fused with the perichondrium of Meckel's cartilage in the articular region.

The ethmoid ossification (eth) in the membrane dorsal to the ethmoid plate has a dorsomedian ridge. It is fused with the perichondrium of the ethmoid plate in the nasal region. The perichondral ossification is present only on the dorsal surface of the ethmoid plate.

The lateral ethmoid (let) has appeared as a vertical intramembranous ossification in front of and continuous with the perichondrium of the lamina orbitonasalis. It has also a lateral extension forming the posteroventral wall to the nasal sac. The perichondral ossification extends medially on the dorsal and ventral surfaces of the short solum nasi in the posterior region of the nasal capsule.

The sphenotic (sph) has developed in the lower part of the postorbital process and the anterior part of the auditory capsule as perichondral bony lamella. Laterally where the hyomandibula articulates, the perichondral ossification is continuous with an intramembranous extension which affords surface for the attachment of the adductor muscles of the hyomandibula.

The pterotic (pto) is ossifying on the ventral surface of the otic capsule covering the large fenestra basicapsularis. Laterally the intramembranous lamina is continuous with the ventral perichondrium of the capsular cartilage. The prootic develops as perichondral lamellae on the dorsal and ventral surfaces of the basal plate anteriorly at the level of the lateral commissure. The ossification is not extensive at this stage.

The epiotic (epo) ossification is observed in the dorsoposterior region of the otic capsule in the perichondrium on both the surfaces.

The supraoccipital (soc) has a very large intramembranous ossification forming the roof of the cranial cavity in the auditory and occipital regions. Only a small part of the bone anteriorly is in continuity with the perichondrium of the short

taenia tecti medials. The lateral margin of the supraoccipital is bifurcated embracing the epiotic between its limbs.

The exoccipital (exo) has ossified from two centres. One of them lies in the membrane on the inner dorsal surface of the cartilage in front of the tectum posterius. This intramembranous ossification more posteriorly is continuous with the inner perichondrium of the occipital cartilage. Posterolaterally there is another centre with a perichondral and an intramebranous extension, the latter overlooking the foramen for the ninth and tenth cranial nerves.

The basioccipital ossification has appeared anteriorly in the median line covering the mesial edges of the parachordals. The ossification extends laterally and posteriorly surrounding the anterior tip of the notochord.

In the lower jaw, the retroarticular (ret) commences as perichondral ossification around the lower edge of the short retroarticular process (ra) of Meckel's cartilage.

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The intramembranously ossified part of the quadrate has a canal ventrally, in which the anterior part of the hyosymplectic cartilage was noticed in the earlier stages. The ventral limb of the quadrate has extended dorsally and ventrally. The dorsal extension anteriorly is continuous with the perichondral part extending the entire height of the cartilage except in its dorsal border which is covered by the entopterygoid bone.

The symplectic has further ossified in the membrane in the lateral wall of the oral cavity in the nasal region. Posteriorly the perichondral part of the symplectic is separated from the hyomandibular ossification by a cartilaginous unossified zone. The hyomandibular cartilage has been replaced by a bony lamella which encloses the foramen for the ramus hyomandibularis facialis. On the inner surface the hyomandibula has an intramembranous extension.

The copula communis is covered with a thin perichondral ossification of the basihyal (bhy) in front of its articulation with the hypohyals. In front of and behind the basihyal the copula is cartilaginous. The hypohyal (hyh) and the ceratohyal (cyh) arise perichondrally in their respective cartilages and are associated with intramembranous extensions. The epihyal (ehy) ossifies in the dorsal perichondrium of the ceratohyal cartilage beneath the stylohyal. The stylohyal (shy) at its articular surface with the epihyal is ossifying in the perichondrium of its cartilage.

No ossification is observed in the branchial arches.

Stage F: 83.0 mm. total-length young fish. (Figs. 10, 11).

While there has been a general growth of the bones that have already developed as described in the preceding stage, a few additional bones have appeared as could be seen by comparing figures 9 and 10. I shall refer to the new bones that have developed in this stage and to the main changes that have occurred in others.

The membrane bones that have developed in this stage are the posttemporal,

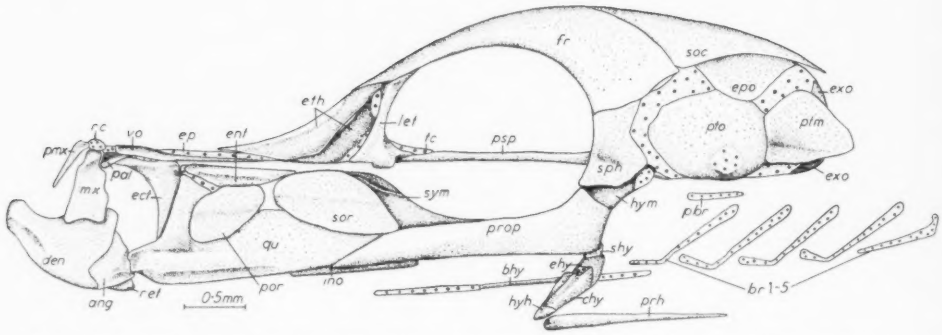

Fig. 10. Lateral aspect of the developing osteocranium of *Nerophis* young, 83 mm long. Cartilage shown by large dots.

the interopercle, the subopercle, the parahyoid and two bones corresponding to the suborbital series of bones of other teleosts. I have called the posterior of the two bones the suborbital (Fig. 10, sor) and the other the preorbital (por).

The posttemporal (ptm) develops outside the cartilage in the postero-lateral aspect of the auditory capsule as a thin scale-like bone below the integument. Anteriorly it overlaps the pterotic and posteriorly it projects beyond the occipital region.

The interopercle (ino) is a flat thin bone lying on the lower inner surface of the posterior region of the quadrate and the anterior region of the preopercle (prop). The subopercle ossifies as a thin bony lamella on the inner lower margin of the opercle.

The parahyoid (prh) has ossified in the ligament posterior to the hypohyals as a long bony rod.

The suborbital (sor) is a thin intramembranous ossification below the skin. Anterodorsally it comes in contact with the posterior end of the entopterygoid (ent), ventrally with the quadrate (qu) and touches the preopercle (prop) posteriorly. It covers the vertical plate of the symplectic partially but is separated from it by muscles.

Anterior to the suborbital there is a similar small scale-like bone, the preorbital (por) overlapping the anterior part of the quadrate. Its dorsal margin is connected to the entopterygoid. A small gap is left between the preorbital and the suborbital which is covered by a membrane.

A small scale-bone (not shown in the figure) has developed beneath the sphenotic covering the hyomandibula affording attachment to the muscles of the operculum.

Amongst the cartilage bones, the palatine (pal) has ossified in the perichondrium of the pterygoid process of the quadrate cartilage. The posterior end of the cartilage is unossified and lies in a deep groove on the dorsal surface of the ectopterygoid bone.

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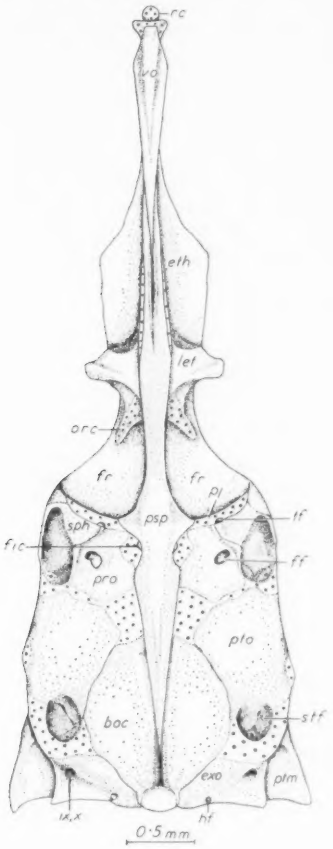

Fig. 11. Ventral aspect of the developing osteocranium of *Nerophis* young, 83 mm long. Jaws not shown. Cartilage shown by large dots.

The ethmoid cartilage (ep) is seen still persisting as a continuous axial structure of the snout. The ethmoid bone (eth) has larger lateral extensions over the dorsal surface of the cartilage anteriorly. KINDRED (1924) stated that the entire ethmoid plate in *Syngnathus* is enclosed in a perichondral sheath of bone. The perichondral ossification in *Nerophis* is found only in the nasal region ensheathing the cartilage except on the ventral surface.

The pteroctic (pto) now forms a greater part of the lateral wall and floor of the auditory capsule. Ventromedially its is connected to the basioccipital and dorsally to the epiotic. It is not yet sutured with the prootic and the sphenotic as the cartilage still persists between them. Between the outer and inner perichondral bony lamellae the cartilage still persists inside the pterotic bone.

The prootic (Fig. 11, pro) which was small in the previous stage, has extended posteriorly in the basal plate in the present stage enclosing the foramen for the

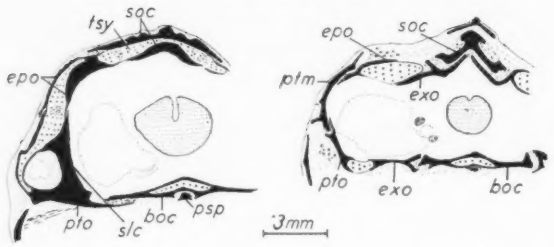

Fig. 12. Fig. 13.

Fig. 12. Transverse section of the skull of *Nerophis* young, 113 mm long in the auditory region. Jaws etc. not shown.

Fig. 13. Transverse section of the skull of *Nerophis* young, 113 mm long in the posterior part of the auditory region. Jaws etc. not drawn.

facial nerve. The prootics of the two sides are separated medially by a strip of cartilage of the prootic bridge beneath which the parasphenoid lies.

The epiotic (Fig. 10, epo) is overlapped by the supraoccipital and ventrally it is suturally connected with the pterotic.

The basioccipital (Fig. 11, boc) is very large ossifying in the dorsal and ventral perichondria of the posterior half of the basal plate. The ossification sorrounds the notochordal sheath below the foramen magnum giving rise to the condyle.

The supraoccipital (Fig. 10, soc) extends upto the tectum posterius but does not ossify in it. The lateral borders of the bone have invaded the perichondrium of the otic capsule at certain places and at others they merely overlap and extend into the membrane.

The quadrate (Fig. 10, qu) has increased in height behind the perichondral part and is overlapped by the preorbital and the suborbital bones. Posteriorly the narrow part of the bone is completely covered by the preopercle which also covers the symplectic and the hyomandibula.

In the hyomandibula (hym), cartilage persists inside the bone and also at the region of its articulation with the auditory capsule and the opercle. The sphenotic, the preopercle and the scale-bone between the sphenotic and the opercle cover the hyomandibula on the lateral aspect.

The posterior end of Meckel's cartilage below the articular region is covered by perichondral ossification of the retroarticular bone (ret). It is covered laterally by the angular (ang).

The hypo-, cerato-, epi- and stylo-hyals enclose their respective cartilages inside the perichondral ossifications.

A pair of branchiostegal rays has made its appearance in the membrane along the inferior margin of the opercle.

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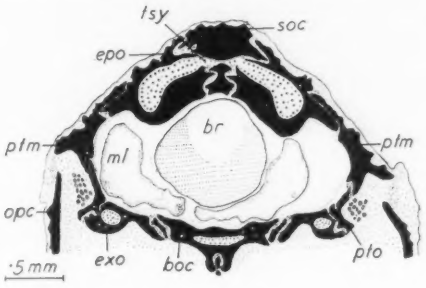

Fig. 14. Transverse section of the adult skull of *Syngnathus serratus* in the posterior part of the auditory region. Jaws etc. not drawn.

Stage G: 113.0 mm. total-length young fish.

The ossification of the skull is almost complete and the cartilage persists only in a few regions in some of the bones. The adult skull of *Nerophis* has been figured by JUNGERSEN (1910, Pl. 5, figs. 9, 10).

The only additional cartilage bone which has appeared in this stage is the pleurosphenoid. It has been observed that the replacing bones develop perichondrally and increase in thickness as the cartilage gradually shrinks and ultimately disappears. No endochondral ossification is seen in any case.

The ethmoid region: The ethmoid cartilage which hitherto formed a continuous axial structure has atrophied in the middle of the snout in front of the ethmoid bone. The distal part of the cartilage with the preethmoid cornu is retained on the dorsal surface of the vomer. The proximal part has ossified into the ethmoid bone. The anterior part of the ethmoid ossification is purely intramembranous and does not invade the cartilage which was below it and which is resorbed as mentioned above. In the nasal region the ethmoid bone forms the nasal septum having ossified in the perichondrium of the cartilage. The interior of the bone is filled with cartilage. The lateral intramembranous extensions of the ethmoid bone form the floor and roof of the nasal sacs.

The preetmoid cornua show partial ossifications at the region of articulation with the palatines. These ossifications are continuous with the vomer posteroventrally.

The lateral ethmoid ossifies in the lamina orbitonosalis and the posteroventral part of the ethmoid cartilage. It has anteriorly an intramembranous ossification fused with the perichondrium of the lamina orbitonasalis. The ventroposterior ends of the lateral ethmoid extend in the membrane on either side of the short trabecula communis and are attached to the lateral surface of the parasphenoid in the anterior region of the orbit.

A very short anterior myodome may be said to exist since between the lateral ethmoids and behind the nasal septum a small space is enclosed being divided by the interorbital septum to which a few muscle fibres of the eye-muscles are attached. This space opens posteriorly into the orbit.

In front of the ethmoid bone the dorsal surface of the snout is formed by the vomer as the cartilage has disappeared as mentioned before. The posterior half of the vomer lies below the ethmoid bone and the parasphenoid. The vomer does not extend into the nasal region. As in *Nerophis* the vomer is less extensive in *Gastrotoceus* (Fig. 16, vo) than in *Hippocampus* (Fig. 19, vo) and *Syngnathus* (Fig. 15, vo) where the vomer extends further backwards upto the posterior part of the nasal region.

The orbito-temporal region: The roof is formed by the two large frontals which are narrow anteriorly and broad posteriorly. The anterior ends overlap the posterior border of the ethmoid bone and the lateal ethmoids. Behind the orbit, the frontal overlaps the dorsal region of the sphenotic and encloses a fragmented piece of cartilage of the postorbital process. Posterliorly the frontal overlaps the supraoccipital and the anterodorsal border of the pterotic.

The frontal (fr) in *Hippocampus* (Figs. 18, 20) and *Gastroceus* (Fig. 16) is provided with a well developed blunt spine in the superior posterior border of the orbit. In *Syngnathus* (Fig. 15) the spine is low and serrated.

The parasphenoid in *Nerophis* (see fig. 11, psp) is a very long bone in the floor of the skull extending from the ethmoid to the occipital region. In the middle it is broad with lateral ascending processes which meet the pleurosphenoid and prootic on each side. The posterior "myodome" for the recti muscles of the eye is formed between the ascending wings of the parasphenoid. There is no bony roof to the "myodome". The carotid artery enters the cranium trough a foramen (fic) situated between the parasphenoid and the prootic in the posterior part of the "myodome" as in *Hippocampus* (Fig. 19, fic), *Syngnathus* and *Gastrotoceus*.

The pleurosphenoid which has ossified in the 113 mm. stage of *Nerophis* in the perichondrium of the pila lateralis and a part of the postorbital process, forms the posterior wall to the orbit along with the sphenotic. The pleurosphenoid is wedged between the sphenotic, the parasphenoid and the prootic. The cartilage of the postorbital process is seen persisting between the perichondral bony lamellae. KINDRED (1924) does not refer to the presence of the pleurosphenoid in *Syngnathus fuscus*. I have been able to discover the bone in all the syngnathids that I have examined (Fig. 20, pls).

The suborbital chain of bones of other teleosts is represented in *Nerophis* by two bones lying one in front of the other. Forming the antero-inferior border of the orbit there is a large scale-like bone, the suborbital. It covers the symplectic laterally almost completely and ventrally it comes in contact with the preopercle. In front of the suborbital there is the other broad scale-like bone, the preorbital. The gap between the two bones noticed earlier (Stage F) is covered by the further growth of the preorbital. This bone covers the anterior region of the quadrate and the entopterygoid. While there is a single preorbital in *Nerophis*, in *Syngnathus* (Fig. 15), *Gastrotoceus* (Figs. 16, 17) and *Hippocampus* (Figs. 21, 22) there are two preorbitals (por″, por′) in front of the suborbital (sor). The anterior

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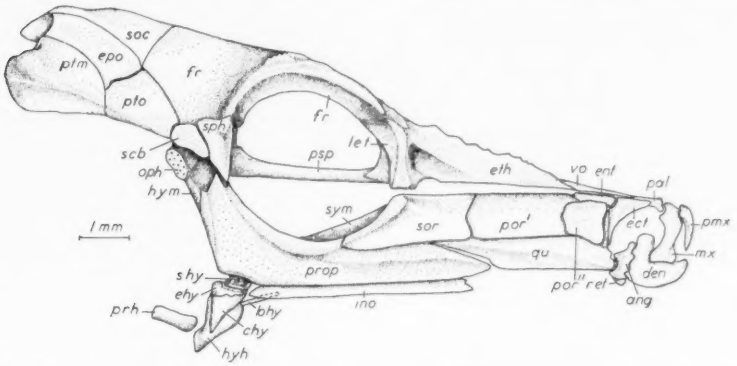

Fig. 15. Lateral aspect of the adult skull of *Syngnathus serratus*. Branchial skeleton, opercle and subopercle not shown.

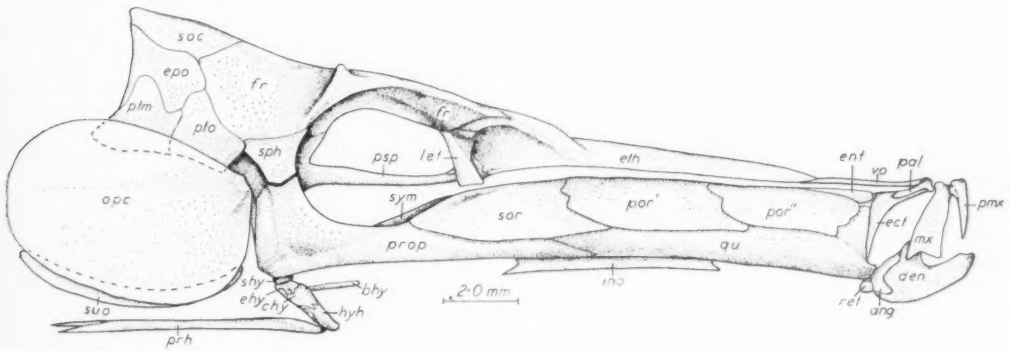

Fig. 16. Lateral aspect of the adult skull of *Gastrotoceus biaculeatus*.

preorbital (por″) in *Hippocampus* and *Syngnathus* is small and scale-like while in *Gastrotoceus* it is elongated and resembles the posterior preorbital (por′).

The auditory region: Behind the orbit the sphenotic forms the posterior border of the orbit and the anterior wall of the auditory capsule. The perichondral ossification of sphenotic does not extend to the dorsal extremity of the postorbital cartilage as the cartilage in this region is showing signs of degeneration. The sphenotic anteroventrally is connected with the pleurosphenoid and the prootic. Much of the cartilage in the postorbital process is replaced by perichondral ossification except in the region of suture of the sphenotic with the pleurosphenoid where the cartilage persists and shows a zone of flattened cells indicating the border between the two bones. Ventrolaterally the sphenotic has a depression for the articulation of the hyomandibula.

The pterotic is an extensive bone forming the lateral wall and floor of more than half of the auditory capsule. The perichondral ossification of the cartilage

is complete and there is no intramembranous ossification associated with the bone. In *Gasteorsteus* (SWINNERTON, 1902) the pterotic has an intramembranous ossification. The only septum of the labyrinth (Fig. 12, slc) belonging to the lateral semicircular canal has ossified in the pterotic bone in the 113 mm. stage of *Nerophis*. The bone is bounded anteriorly by the sphenotic and the frontal, dorsally by the epiotic and posteriorly by the posttemporal and posteroventrally by the exoccipital and the basioccipital.

The epiotic forms the dorsolateral wall of the otic capsule between the pterotic and the supraoccipital. The cartilage that persits in the interior of the bones shows a zone of flattened cells at the sutural region of the bones (Fig. 12). Posteriorly the epiotic is in contact with the posttemporal and the exoccipital.

The posttemporal is a membrane bone which covers the lateral surface of the auditory capsule behind the pterotic. It is interesting to note that in this region since a part of the cartilage of the otic capsule is resorbed, the posttemporal actually takes part in the formation of a portion of the capsular wall. The gap that is covered by the posttemporal lies between the epiotic above and the pterotic below (Fig. 13). Further behind where the exoccipital forms the complete wall, the posttemporal overlaps that bone and extends posteriorly as a process beyond the occipital region of the skull. In *Syngnathus* also the posttemporal (Fig. 14, ptm) is seen to form a part of the auditory capsule between the epiotic (epo) and the pterotic (pto). In *Hippocampus* the posttemporal (Fig. 18, ptm) carries a prominent spine on the dorsal surface like the frontal. Ventrally the anterior part of the posttemporal forms the lateral margin of the subtemporal fossa (Fig. 19, stf).

The occipital region: Only the two exoccipitals are restricted to the posterior region of the skull, while the supraoccipital and the basioccipital extend far forwards into the roof and floor of the skull respectively. The supraoccipital is a large bone forming the roof of the cranium behind the frontals. It ossifies largely in the membrane and has perichondral extensions in the posterior end of the taenia tecti medialis and partially in the dorsal border of the capsular cartilage in front of the epiotic. A tectum synoticum which is absent in the earlier stages has developed in the posterior region of the auditory capsule and the supraoccipital ossification has extended in the perichondrium on both the surfaces of the tectum (Fig. 12, tsy). A tectum synoticum which is not seen in the earlier stages of *Syngnathus* (KINDRED, 1921, 1924) is present in an adult skull of *Syngnathus serratus* which I have cut and examined and the supraoccipital bone encloses the tectum (Fig. 14, tsy) as in *Nerophis*.

In both *Syngnathus* (Fig. 15) and *Hippocampus* (Figs. 18, 19, 20) the supraoccipital (soc) has a well developed posteriorly directed crest overhanging the foramen magnum. *Gastrotoceus* does not possess a supraoccipital crest.

The exoccipitals in *Nerophis* ossify in the occipital arch and tectum posterius extending in the posterior wall of the auditory capsule. They meet above the

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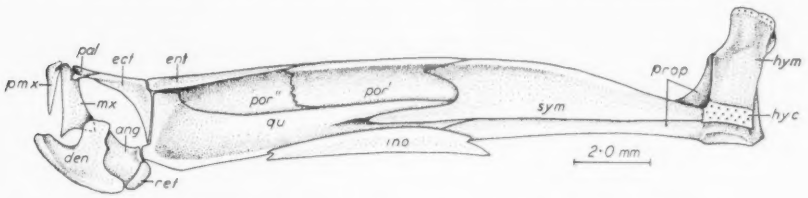

Fig. 17. Mesial aspect of the jaws and suspensorium of *Gastrotoceus biaculeatus.*

foramen magnum excluding the supraoccipital. Ventrally each exoccipital extends forwards meeting the pterotic in the subtemporal fossa. The foramen for the ninth and the tenth cranial nerves lies laterally while the foramen for the first spinal nerve is present more posteriorly on the ventral surface of the bone which has ossified in the membrane. The occipital cartilage persists largely in the region of the foramen magnum as in *Hippocampus* (Fig. 20, occ).

The basioccipital has developed as perichondral lamellae on both surfaces of the basal plate behind the prootic. The basioccipital ossification ensheaths the notochord and extends laterally from it in the basal plate. In front the basioccipital is separated from the prootic by a narrow strip of cartilage; laterally it articulates with the pterotic and the exoccipital. Almost upto its posterior end it is underlaid by the long posterior shaft of the parasphenoid which ends a little in front of the condylar region.

The jaws: The edentulous premaxillae and the maxillae border the gape of the mouth dorsally and laterally. Each premaxilla is a small vertical bone tapering ventrally. Dorsally it is broad and articulates with the rostral cartilage. The maxilla is also vertical and consists of a broad plate of bone, the ventral part of which overlaps the dentary of the lower jaw. Dorsally the maxilla articulates with the rostral cartilage behind the premaxilla and also with the maxillary process of the palatine bone.

The dentaries are large forming more than half of the lower jaw. Anteriorly they meet in the middle by a ligamentous symphysis. The anterior end of Meckel's cartilage is still seen to be continuous with the dentary ossification. Meckel's cartilage still persists in the dentary in a canal anteriorly and in a groove posteriorly on the mesial surface of the bone. In some places the perichondrium is eroded and the cartilage appears to be undergoing resorption. In the posterior region the angular is found on the lateral surface of the cartilage of Meckel and in the articular region the angular is continuous fith the perichondrium surrounding the cartilage. The retroarticular is found on the inner surface of the angular below the articular region ossifying in the perichondrium of the retroarticular process of Meckel's cartilage. The bone shows small anterior and posterior intramembranous extensions.

The palatine may be described as an autopalatine since it ossifies in the cartila-

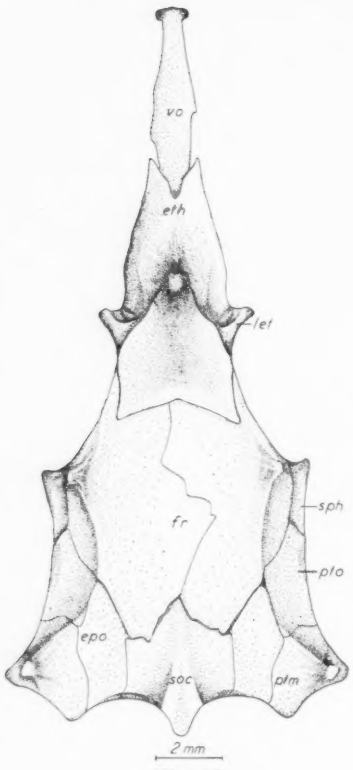

Fig. 18

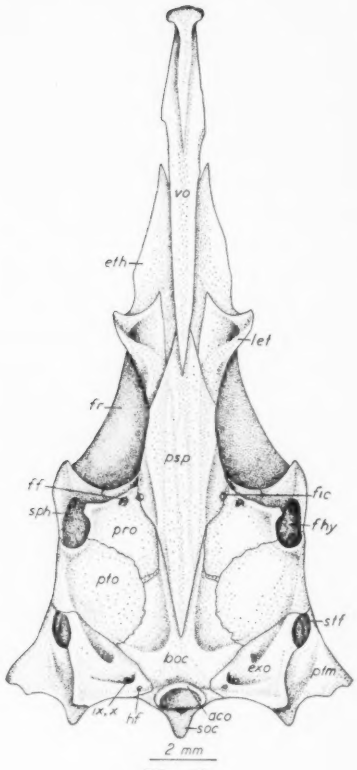

Fig. 19

Fig. 18. Dorsal aspect of the adult cranium of *Hippocampus guttulatus.*

Fig. 19. Ventral aspect of the adult cranium of *Hippocampus guttulatus.*

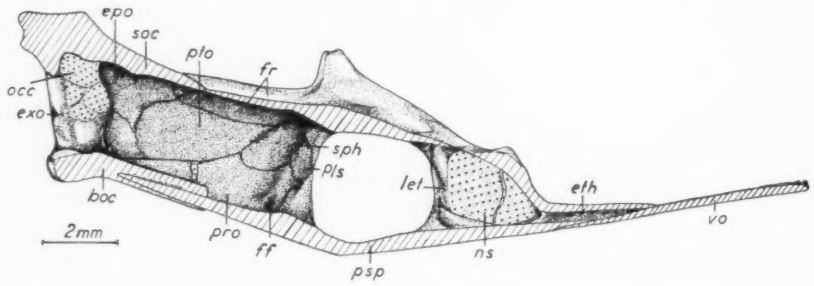

Fig. 20. Mesial sagittal aspect of the adult cranium of *Hippocampus guttulatus.*

ginous pterygoid process of the quadrate. The anterior head of the pterygoid has a lateral maxillary process and a medial vomerine process. Posteriorly the bone is narrow and lies in a groove on the dorsal surface of the ectopterygoid bone.

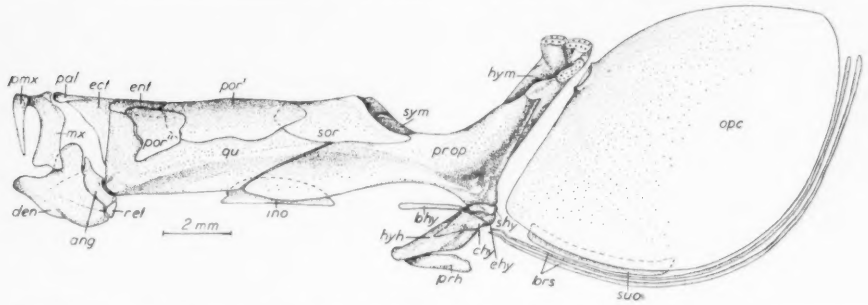

Fig. 21. Lateral aspect of the jaws, the suspensorium and opercular bones of *Hippocampus guttulatus.*

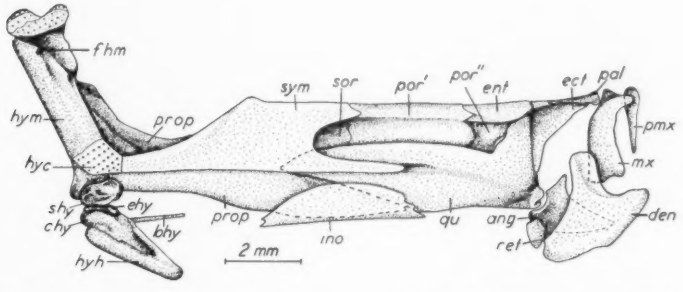

Fig. 22. Mesial aspect of the jaws and the suspensorium of *Hippocampus guttulatus.*

The ectopterygoid connects the palatine and the anterior face of the quadrate. The entopterygoid articulates anteriorly with the posterior end of the ectopterygoid. The entopterygoid extends along the dorsal border of the quadrate to the anterodorsal process of the symplectic. In the anterior region the bone is in close contact with the quadrate cartilage which shows signs of degeneration. The dorsal border of the preorbital and suborbital overlap the lower border of the entopterygoid.

KINDRED (1924) described a single pterygoid in *Syngnathus.* In the skulls of *Syngnathus* (Fig. 15) examined by me there are two distinct pterygoids, the ectopterygoid (ect) and the entopterygoid (ent). They are also present in the other two genera examined; (*Hippocampus,* figs 21, 22; *Gastrotoceus,* figs 16, 17, ect. ent).

In *Nerophis* the quadrate is broad and long forming a greater part of the anteroventral half of the snout region. Most of the cartilage has ossified and only a slender core of cartilage is present in the anterior region of the quadrate. This region is covered by the preorbital. The ventral part of the bone contains a canal which opens out into a groove mesially for the anterior end of the symplectic

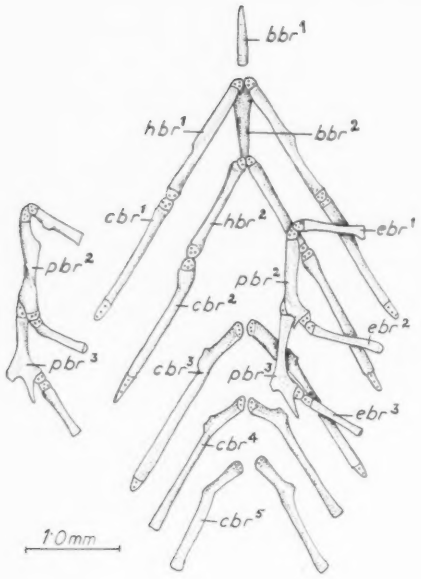

Fig. 23.

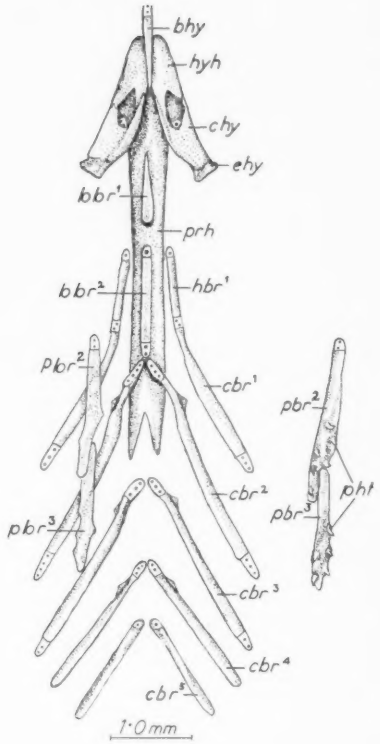

Fig. 24.

Fig. 23. Dorsal aspect of the branchial skeleton of *Syngnathus serratus*. Right dorsal half reflected.

Fig. 24. Dorsal aspect of the hyobranchial skeleton of *Gastrotoceus biaculeatus*. Left pharyngobranchs reflected.

which is tipped with cartilage. The posterior part of the quadrate narrows and is wedged between the preopercle laterally and the symplectic mesially. Anteroventrally the quadrate articulates with the angular of the lower jaw.

The horizontal symplectic of the hyosymplectic cartilage except distally ossifies into the symplectic bone which has a large vertical intramembranously ossified plate with an anterodorsal process. The vertical plate of bone decreases gradually in height behind the nasal region and forms the lower border of the orbit. Laterally it is covered by the suborbital and the preopercle. Posteriorly the symplectic is separated from the hyomandibula by a stout intervening cartilaginous zone. The hyomandibula in its ventral half consists of thin perichondral bony lamella surrounding the cartilage. The head of the hyomandibula articulating with the sphenotic and the pterotic, and the opercular process of the hyomandibula have cartilaginous epiphyses. The rest of the cartilage has ossified giving rise

to the hyomandibular bone. On the inner surface there is an intramembranous extension of the bone coming in contact with the pterotic.

The hyobranchial skeleton: The hyoid cornu consists of the stylohyal, epihyal, ceratohyal and hypohyal bones. A parahyoid extends posteriorly from the hypohyals ventral to the branchial arches. The rod-like basihyal lies in front of the hypohyals tipped with a long cartilaginous copula. The branchial arches for the most part are still cartilaginous. Only in the first arch perichondral ossifications are noticed in the hypobranchs which are widely separated from the cartilaginous ceratobranchs. The basibranch of the first arch lies behind the basihyal and has ossified in the posterior part of the cartilaginous copula.

A pair of slender branchiostegal rays is present. Anteriorly the rays are attached to the epihyals. In *Hippocampus* (Fig. 21) and *Syngnathus* there are two pairs of branchiostegal rays (brs).

The opercular series consists of the opercle, the preopercle, the subopercle and the interopercle. The opercle is thin and vaulted articulating with the hyomandibula on the opercular process. The subopercle is a thin bone covering the mesial lower border of the opercle. The preopercle is the stoutest bone of the series with a vertical limb covering the hyomandibula and a horizontal limb covering the symplectic bone. Along with the latter the preopercle forms the lower border of the orbit. The interopercle is an elongated narrow splint-like bone lying on the inner surface of the quadrate and the preopercle at the region of their suture. The interopercle is attached to the lower jaw and to the hyoid posteriorly. In *Syngnathus* (Fig. 15) the interopercle (ino) is highly elongated and extends the entire length of the ventral border of the preopercle upto the stylohyal. In *Gastrotoceus* (Figs. 16, 17) and *Hippocampus* (Figs. 21, 22) the interopercle (ino) lies between the quadrate and the preopercle as in *Nerophis*.

As in *Hippocampus* (JUNGERSEN, 1910) the epibranchs of the first three arches are widely separated from their corresponding ceratobranchs in *Syngnathus* (Fig. 23, ebrl-3). The first and second epibranchs are attached to the anterior and posterior ends of the second pharyngobranch (pbr2) respectively. The third epibranch is connected to the posterior end of the third pharyngobranch (pbr3). While there are no medial elements in the branchial skeleton of *Hippocampus*, in *Syngnathus* there are two basibranchs (bbrl-2) in the first two arches. In *Gastrotoceus* (Fig. 24) there are two basibranchs and two pairs of Pharyngobranchs as in *Syngnathus* but no epibranch in any arch as in *Nerophis*. The pharyngobranchs of *Gastrotoceus* are peculiar in possessing pharyngeal teeth (pht) on their inferior surfaces. The hypobranchs (hbrl) are present only in the first arch.

DISCUSSION

The ethmoid bone in *Nerophis* develops in front of the nasal region as an intramembranous ossification overlying the cartilage. In the nasal region the dermal

ossification is fused with the perichondral ossification. Though the cartilage is present below, the dermal ossification does not invade the cartilage which, however, is resorbed in later stages. Thus the anterior part of the ethmoid bone represents the primitive supraethmoid ossification co-ossifying with the perichondral ethmoid ossification. In *Syngnathus fuscus* KINDRED (1924) described the ethmoid ossification as perichondral bone surrounding the entire length of the ethmoid cartilage in front of the nasal region. He also recognised a dermal ossification fused with the dorsal surface of the perichondral ossification in the nasal region. In the adult skulls of *Syngnathus serratus* (Fig. 15), *Gastrotoceus biaculeatus* (Fig.16) and *Hippocampus guttulatus* (Figs. 18, 19, 20) and other lophobranchiate skulls (JUNGERSEN, 1910; GREGORY, 1933) the ethmoid (mesethmoid of other authors) bone does not extend the entire length of the snout, the anterior part of the snout being always formed by the vomer. In *Nerophis* and *Syngnathus* I have noticed the resorption of the ethmoid cartilage in front of the ethmoid bone. Only the distal part of the ethmoid cartilage with preethmoid cornua persists in the adult.

In some of the teleosts the two bones—the dermal supraethmoid and the cartilaginous ethmoid bones—remain distinct as in Gobioninae (RAMASWAMI, 1955 a) or they may be fused into a single bone in the same family as in Cyprininae (RAMASWAMI, 1955 b). In *Salmo* DE BEER, 1937) and *Gasterosteus* (SWINNERTON, 1902) the two ossifications are fused from the beginning as in *Nerophis*. SRINIVASACHAR (1958) has reported only the perichondral ossification of the ethmoid bone in the catfish *Heteropneustes*.

The anterior extent of the ethmoid bone varies in different syngnathids. In *Siphonostoma* and *Solenostomus* (JUNGERSEN, 1910) the ethmoid (mesethmoid) makes up more than half the length of the snout. While in *Hippocampus* and *Nerophis* the ethmoid is not so extensive, in *Gastrotoceus* it is highly elongated comprising nearly three fourths of the dorsal region of the snout as in *Phyllopteryx*.

Describing the pterygoid in *Syngnathus fuscus,* KINDRED (1924) stated that the bone extended on the dorsal margin of the pterygoquadrate cartilage and sent down a spur which overlapped the anterior face of the quadrate cartilage. He further stated that the posterior margin of the pterygoid was overlapped by the metapterygoid. In the skulls of *Syngnathus* examined by me the pterygoid consists of two distinct bones, the ectopterygoid and the entopterygoid. The former bone lies in front of the quadrate and corresponds to the "spur" which overlaps the anterior face of the pterygoquadrate cartilage of Kindred's description. The entopterygoid lies behind the ectopterygoid dorsally to the quadrate bone. Developmentally also the two bones ossify separately in *Nerophis*.

A metapterygoid is absent in the syngnathids according to JUNGERSEN (1910) and BERG (1947). However, DE BEER (1937) agreeing with KINDRED's description (1924) of the metapterygoid in *Syngnathus fuscus* has questioned whether the bone has arisen as an intramembranous ossification. According to me, the so-

called metapterygoid is one of the bones corresponding to the suborbital series of other teleosts and therefore a metapterygoid is absent confirming the observations of Jungersen and Berg. The lack of sensory canals in the syngnathids has added to the confusion. As JUNGERSEN (1910, p. 300) has correctly pointed out, the bone lies outside the muscles, develops as a thin scale-like bone below the dermis late in ontogeny and is in no way connected with the pterygoquadrate cartilage. The bone labelled as metapterygoid in *Syngnathus* by Kindred, I have ventured to call a preorbital (Fig. 15, por′). The anterior preorbital (por″) described by me probably had not yet ossified in the specimen described by Kindred. When ossified it would occupy the gap shown in front of "meta pterygoid" in Plate 1, figs. 1, 2, figured by KINDRED (1924).

Corresponding to the suborbital chain of bones of other teleosts, in the syngnathids there are two or three flat bones covering the lateral surface of the snout in front of the orbit. These bones develop late as intramembranous ossifications and overlap the bones of the upper jaw series. In the antero-inferior angle of the orbit there is a large bone designated by me as the suborbital (sor) since in its position and relationship it corresponds to the suborbital of other teleosts. The bone has been labelled as infraorbital in *Syngnathus* (KINDRED, 1924), *Siphonostoma* (*Syngnathus*) (BERG, 1947), and preorbital or antorbital by JUNGERSEN (1910). In front of the suborbital there are one or two bones, the preorbitals. In *Nerophis* and *Siphonostoma* there is only one large preorbital while in *Hippocampus, Syngnathus* and *Gastrotoceus* there are two preorbitals. The preorbitals and the suborbital have been incorrectly labelled as "mtp" (metapterygoid) in *Phyllopteryx* by GREGORY (1933, fig. 106).

The vomer in *Nerophis* arises as a single median bone and lies in front of the ethmoid. Its anterior end is broader carrying the preethmoid cornua for the articulation of the palatines and maxillary bones. The front end of the vomer ossifies below the preethmoid cornua of the ethmoid plate and later the ossification invades the ventral perichondrium and is continous with it as in *Exocoetus* (LASDIN, 1913). The lateral processes (preethmoid cornua) have also been observed to have partially ossified. These ossifications might suggest the preethmoid bones present in some teleosts like *Esox* (SWINNERTON, 1902), *Eventognathi* (STARKS, 1926) and *Cyprinoids* (RAMASWAMI, 1955 b). In *Syngnathus serratus* my sections of the adult skull reveal the presence of nodule-like ossifications in the preethmoid horns continuous with the vomer below. Posteriorly the vomer is interpolated between the ethmoid and the parasphenoid bones. The vomer in *Nerophis* and *Gastrotoceus* which belong to Gastrophori (BERG, 1947) does not reach the nasal region but ends far in front unlike in members of Urophori (*Hippocampus, Syngnathus* and *Siphonostoma*) where the vomer extends posteriorly to the level of the lateral ethmoids. In *Solenostomus* (JUNGERSEN, 1910) the vomer underlies only the foremost part of the ethmoid and ends in front of the parasphenoid as in *Fistularia* and *Aulostoma*.

In front of the auditory region, the orbital wall is formed by the parasphenoid, the prootic, the sphenotic and the pleurosphenoid. The last mentioned bone is small and was missed by Kindred and Swinnerton as they did not mention about it. In *Nerophis* the pleurospenoid ossifies completely in the postorbital process in front of the prootic ossification in the lateral commissure. JUNGERSEN (1910) has described this bone as "alisphenoid" in *Siphonostoma* and as the alisphenoid is restricted to mammals, I have called it pleurosphenoid following DE BEER (1937). It is present in all the syngnathids examined by me.

The postero-lateral wall of the auditory capsule in *Nerophis* is covered by a membrane bone, the posttemporal which overlaps the pterotic in front, the epiotic above and the exoccipital behind. Between the pterotic, the epiotic and the exoccipital a part of the cartilaginous wall has disappeared and the gap is covered by the posttemporal. Thus, the posttemporal actually forms a part of the auditory capsule which is a peculiar condition not observed in other teleosts. In *Syngnathus serratus* also I have noticed a similar condition. Kindred does not refer to the posttemporal ossification in *Syngnathus fuscus* (45 mm stage). In *Hippocampus* and *Gastrotoceus* the posttemporal does not appear to form a part of the auditory capsule, but merely overlaps it. Therefore, the doubtful homology of this bone expressed by MCMURRICH (1883) whether the posttemporal was homologous with the supratemporal of *Amia* seems to be justified. However, I have retained the term "posttemporal" having regard to the priority as the bone has been labelled throughout as posttemporal by Jungersen, Gregory and others.

None of the previous workers has mentioned about the septa of the semicircular canals in the otic capsule. In *Nerophis*, the cartilaginous septum of the lateral semicircular canal becomes ossified in the pterotic bone. In the adult skulls of *Syngnathus* and *Gastrotoceus* that I have examined a single septum as in *Nerophis* is present in the pterotic bone. But in *Hippocampus* no septum either in the adult skull or in the chondrocranium (KADAM, 1958) was observed.

The dentary in *Nerophis* as Schleip (quoted by HAINES, 1938) has shown in *Salmo* and UHLMANN (1921) in *Cyclopterus* begins to ossify at an early stage as a single continuous plate of bone which, at the anterior end of Meckel's cartilage, is continuous with the perichondrium. KINDRED (1924) described the angular as perichondral bone and called it the articular. In *Nerophis* the angular originates as a membrane bone and extends into the perichondrium of Meckel's cartilage as HAINES (1938) has pointed out in several teleosts. The bone described as angular by Kindred is apparently the retroarticular.

The branchial skeleton of the syngnathids studied offers an interesting variation and is very much reduced as observed by GOODRICH (1909). A comparative study of the branchial skeletons of *Solenostomus, Siphonostoma, Syngnathus, Nerophis* and *Hippocampus* has been made by JUNGERSEN (1910). The branchial skeletons of *Nerophis* and *Hippocampus* have not been figured in this paper as they have been already done by JUNGERSEN (Pl. VI, figs. 11, 12). Though he states that

the branchial apparatus of *Siphonostoma* is like that of *Syngnathus,* I have noticed certain differences in the species examined by me and hence the branchial skeleton of *S. serratus* has been figured (Fig. 23). There is a greater similarity between the branchial skeletons of *Hippocampus* and *Syngnathus.* In the first branchial arch of *Syngnathus* a hypobranch is present which is said to be absent by Jungersen in *Siphonostoma.*

The branchial skeleton of *Gastrotoceus* shows greater reduction of the branchial elements and is nearer to *Nerophis.* In both the forms the hypobranchs are present only in the first arch. The epibranchs are absent in all the arches. In *Gastrotoceus* the two pharyngobranchs present belong to the second and third arches while in *Nerophis* there is a single pharyngobranch probably representing the fused second and third pharyngobranchs. The most interesting feature of the pharyngobranchs of *Gastrotoceus,* not encountered in other syngnathids studied, is the presence of teeth on their pharyngeal aspect. In this important feature *Gastrotoceus* is nearest to *Solenostomus.* Further, in *Solenostomus* and *Gastrotoceus* the parahyoid (urohyal) is long and bifurcated posteriorly. The hypobranchs do not meet midventrally in both the forms as in *Hippocampus.*

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Summary

The chondrocranium: Six stages in the development of the chondrocranium of *Nerophis* have been studied. The trabecula communis is highly elongated and might have arisen as a single chondrification. More than half of the ethmoid plate is bent upwards and backwards in early stages and it straightens later. The nasal septum and the laminae orbitonasales arise together independently of the ethmoid plate fusing with it later. The lateral commissure is also a single independent chondrification and it fuses with the auditory capsule and the parachordal. In the auditory capsule there is a stout vertical cartilaginous septum of the lateral semicircular canal. There is no tectum synoticum but a slender tectum posterius is present in the posterior occipital region. The only other roofing cartilage is a small triangular piece of cartilage in the hind part of the orbital region.

Meckel's cartilages are obliquely vertical in earlier stages and rotate later into horizontal position. The pterygoid process of the quadrate arises independently and remains so without becoming continuous with the quadrate. There is only a rostro-palatine articulation. The hypophyal and ceratohyal of each side are fused anteriorly for a short distance. In the branchial arches, only a pair of pharyngobranchs is present. There are no basibranchs. A rostral cartilage is present in front if the ethmoid plate.

Sclerotic cartilages are present in the optic cups.

An account of general features of the syngnathid chondrocranium is given.

The osteocranium: The ethmoid bone is a chondromembranal one ossifying as an intramembranous bone anteriorly and as perichondral bone posteriorly. The vomer underlies only the anterior part of the ethmoid bone and does not reach the nasal region. The lateral ethmoid is also a chondromembranal bone ossifying in the lamina orbitonasalis with a dermal element added to it.

A part of the postero-lateral wall of the auditory capsule is formed by the post-temporal (supratemporal?). A bony septum of the lateral semicircular canal is present in the pterotic bone which is purely a cartilage bone without any intramembranous ossification. The sphenotic has an intramembranous extension. The supraoccipital is for the most part an intramembranously ossified bone and is related to the cartilage anteriorly and posteriorly to a little extent. The exoccipital has a postero-lateral intramembranous ossification. The basioccipital is entirely a cartilage bone.

The chain of suborbital bones of other teleosts is represented by a suborbital and a preorbital in *Nerophis.* In *Hippocampus, Syngnathus* and *Gastrotoceus* there are two preorbitals in addition to a suborbital.

The jaws are edentulous. The palatine is an autopalatine ossifying in the cartilaginous pterygoid process of the quadrate. The ectopterygoid and the entopterygoid bones are distinct. A metapterygoid is absent. The dentary anteriorly is in close contact with the perichondrium of Meckel's cartilage. The angular posteriorly ensheaths the perichondrium of Meckel's cartilage at the articular region. The retroarticular ossifies in the perichondrium below the articular region and has intramembranous extensions.

The nasals, the orbitosphenoids and the parietals are absent.

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Acknowledgments

I am grateful to Professor T. Pehrson and Dr. L. S. Ramaswami for the material and I also wish to express my sincere thanks to the latter for guidance. I am deeply indebted to Professor B. R. Seshachar for his helpful suggestions and constant encouragement.

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Explanation to abbreviations used

Part. I. Chondrocranium: (Figs. 1—7).

abc	anterior basicapular commissure
ac	auditory capsule
bcf	basicapsular fenestra
br	brain

br1	branchial arches 1—5
br2	
br3	
br4	
br5	
cc	copula communis
ch	ceratohyal
cp	coronoid process
e	eye
ec	preethmoid cornu
ep	ethmoid plate
ff	facial foramen
fme	fissura metotica
hf	hypophysial fenestra
hmf	foramen for the r. hyomandibularis facialis
hyh	hypohyal
hym	hyomandibular portion of the hyosymplectic
hys	symplectic portion of the hyosymplectic
lc	lateral commissure
lon	lamina orbitonasalis
mc	Meckel's cartilage
mp	lateral strand of "mesenchymatous plaque"
mtp	metapterygoid process
nc	notochord
oa	occipital arch
orc	orbital cartilage
pbr	pharyngobranchial
pc	parachordal
pl	pila lateralis
pop	postorbital process of the auditory capsule
pq	palatoquadrate
pt	pterygoid process of the quadrate
qu	quadrate cartilage
ra	retroarticular process
rc	rostral cartilage
sh	stylohyal cartilage
tc	trabecula communis
tf	trigeminal foramen
tm	taenia tecti medialis
tp	tectum posterius
tr	trabecula cranii
ttr	taenia tectum transversum

Part II Osteocranium: (Figs. 8—24).

ac	cartilaginous auditory capsule
aco	articular surface of the condyle
ang	angular
bbr1	basibranchs 1—2
bbr2	

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bhy	basihyal
boc	basioccipital
br	brain
brs	branchiostegal rays
br1	branchial arches 1—5
br2	
br3	
br4	
br5	
c	persisting cartilage
cbr1	ceratobranchs 1—5
cbr2	
cbr3	
cbr4	
cbr5	
chy	ceratohyal
den	dentary
ebr1	epibranchs 1—3
ebr2	
ebr3	
ect	ectopterygoid
ehy	epihyal
ent	entopterygoid
ep	cartilaginous ethmoid plate
epo	epiotic
eth	ethmoid bone
exo	exoccipital
ff	facial foramen
fhm	foramen for r. hyomandibularis facialis
fhy	facet for the articulation of hyomandibula
fic	foramen for internal carotid artery
hbr1	hypobranchs 1—2
hbr2	
hf	hypoglossal foramen
hyc	hyomandibular cartilage
hyh	hypohyal
hym	hyomandibula
ino	interopercle
let	lateral ethmoid
ml	membranous labyrinth
mx	maxilla
occ	occipital cartilage
opc	opercle
orc	orbital cartilage
oph	opercular process of hyomandibula
pal	palatine
pbr	pharyngobranch
pht	pharyngeal teeth
pl	pila lateralis
pls	pleurosphenoid
pmx	premaxilla

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por′	preorbitals
por″	
prh	parahyoid
pro	prootic
prop	preopercle
psp	parasphenoid
pto	pterotic
ptm	posttemporal
qu	quadrate bone
ra	retroarticular process of Meckel's cartilage
ret	retroarticular bone
scb	scale-bone
shy	stylohyal
slc	septum of the lateral semicircular canal
soc	supraoccipital
sor	suborbital
sph	sphenotic
stf	subtemporal fossa
suo	subopercle
sym	symplectic bone
tc	trabecula communis
tf	trigeminal foramen
tsy	tectum synoticum
vo	vomer
IX, X	foramen for the ninth and tenth cranial nerves.

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La morphologie des molaires chez les Equidae *(Ongulés périssodactyles)*, principalement ceux d'Europe. Son évolution phylogénique

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Introduction

Les *Equidae* constituent la famille d'Ongulés périssodactyles la mieux représentée à l'état fossile et la plus spécialisée par ses formes terminales, en sorte que sa phylogénie est un exemple classique de l'évolution.

Les *Equidae* apparaissent à l'Eocène inférieur et atteignent leur apogée avec le genre *Equus* (Cheval) encore actuel. Les sous-familles généralement admises: *Hyracotheriinae, Palaeotheriinae, Anchitheriinae* et *Equinae* représentent surtout des étapes de leur développement.

La dentition de tous les *Equidae* comporte, à chaque hémi-mâchoire: 3 incisives, 1 canine et 6 ou 7 dents jugales. Les *incisives,* aplaties d'avant en arrière, larges et tranchantes, affectent la forme de ciseaux; la *canine,* conique, est séparée des prémolaires par une «barre» qui s'agrandit, au cours des temps géologiques, tandis que s'allongent les os de la face. Les *dents jugales,* d'abord à croissance relativement limitée et à racines nettes, deviennent à croissance continue et les prémolaires tendent à se molariser. La prémolaire antérieure, Pl, toujours plus petite que les autres, a généralement disparu chez l'*Equus* (Cheval) adulte.

La présente étude, faite dans les Collections de Paris, de Montpellier, de Londres et d'Upsal, se rapporte à des molaires non abrasées (seul stade anatomique) de quelques genres d'*Equidae* très typiques. Or, même chez les formes anciennes et archaïques, il est difficile de rencontrer des dents non usées; la chose devient plus difficile encore pour les formes terminales, très évoluées, dont les molaires, à croissance continue, s'abrasent dès leur sortie de l'alvéole.

Ces recherches m'ont été suggérées par un Maître éminent, M. le Docteur M. A. C. Hinton, du British Museum Natural History, au XIIe Congrès International de Zoologie (Lisbonne, 1935).

Je suivrai, ici, le plan esquissé par Ch. Depéret en 1901, pour les *Equidae* d'Europe, en ajoutant quelques formes nord-américaines que j'ai eu l'occasion d'étudier.

Il est certain qu'à plusieurs reprises, au cours des temps tertiaires, l'Ancien Monde fut relié à l'Amérique du nord, ce qui permet d'expliquer l'évolution des *Equidae* sur l'un et l'autre Continents, d'une manière parallèle, mais non pas identique, contrairement à l'opinion de certains Auteurs.

Voici les grandes division de cet exposé:

I. Les *Hyracotheriinae* primitifs.

II. La lignée du *Lophiotherium.*

III. La lignée du *Palaeotherium.*

IV. La lignée de l'*Anchilophus* et de *l'Anchitherium.*

V. La lignée de l'*Equus: Equinae.*

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La morphologie des molaires chez les Equidae

I. Les Hyracotheriinae primitifs

A. HYRACOTHERIUM

L'*Hyracotherium,* envisagé à la manière de Ch. Depéret (1901), c'est-à-dire en excluant toutes les formes américaines qu'on avait voulu y faire entrer, s'affirme comme le plus archaïque des Périssodactyles; il en est aussi le plus ancien (*Eocène inférieur* (London Clay) d'Angleterre).

Ses molaires supérieures, sextuberculées, parabunodontes, possèdent le *type fondamental* à trois rangées longitudinales (externe, intermédiaire et interne) de deux tubercules (M. Friant, 1953, p. 71). Voici, d'ailleurs, la manière dont elles furent décrites, en 1901, par Ch. Depéret, chez l'*Hyracotherium leporinum* Owen: «les 3 molaires supérieures (sont) à six denticules de forme conique, les (2) externes, presque régulièrement coniques, les (2) intermédiaires ayant à peine une tendance à s'allonger en crêtes transversales, les (2) internes, à peu près coniques». Ajoutons à ceci que les tubercules intermédiaires, sensiblement plus petits que les externes et les internes, sont légèrement décalés vers l'avant par rapport à eux.

Aux Collections paléontologiques du British Museum Natural History, j'ai étudié les molaires supérieures de l'*Hyracotherium vulpiceps* Owen (Fig. 1, à gauche), dont les caractères sont les mêmes que chez l'*Hyracotherium leporinum* Owen; toutefois, le tubercule intermédiaire antérieur alterne moins, ici, avec les tubercules externe et interne antérieurs, que chez ce dernier.

Les molaires inférieures de l'*Hyracotherium* présentent aussi le caractère fondamental, à deux rangées, externe et interne, de deux tubercules (Fig. 1, à droite). Au sujet des molaires inférieures de l'*Hyracotherium leporinum,* Ch. Depéret dit: «. . . . de ces quatre (tubercules), les deux internes sont restés coniques, tandis que les deux externes ont une tendance crescentiforme . . .». La 3ème molaire, plus allongée que les autres, possède un talon constituant un 5ème tubercule.

B. PROPACHYNOLOPHUS

Le *Propachynolophus* est connu de l'*Eocène inférieur* de Belgique: Erquelinnes (Hainaut) et de France: Reims, Cuise-la-Mothe (Marne).

Les molaires sont encore de type fondamental, comme celles de l'*Hyracotherium;* cependant, au maxillaire supérieur, les tubercules intermédiaires, plus réduits et allongés, tendent à former une crête transverse avec le tubercule interne correspondant, en particulier sur le jeune exemplaire de *Pachynolophus Gaudryi* Lem. des Collections du Museum de Paris (Fig. 2).

Aux molaires inférieures, les tubercules externes, légèrement en V à sommet jugal, tendent à s'unir en deux crêtes transverses aux internes correspondants.

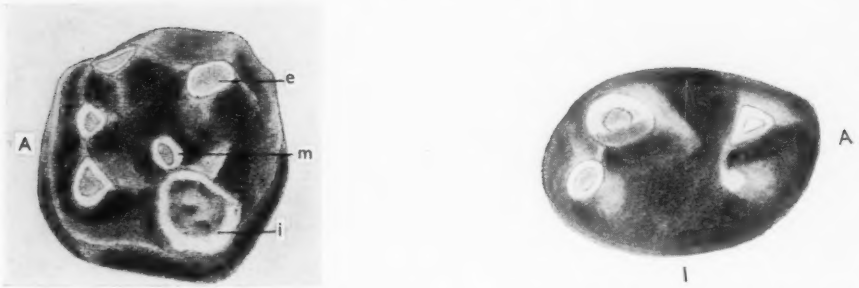

Fig. 1. *Hyracotherium vulpiceps* Owen. Eocène inférieur (London Clay) de Harwich (Essex, Angleterre). Coll. British Mus. N. H. Molaires gauches: *à gauche,* M_1 peu abrasée — e. tubercules externes. — m. tubercules intemédiaires. — i. tubercules internes. — *A droite,* M_1. 5 fois grandeur naturelle environ.

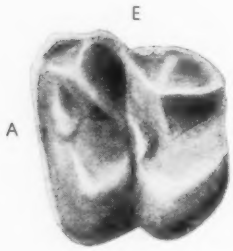

Fig. 2. *Propachynolophus Gaudryi* Lem. Eocène inférieur de Cuise-la-Mothe (Marne). Coll. Museum Paris, Lemoine, 1897—15. Molaire supérieure (M^1) gauche. 2 fois grandeur naturelle environ.

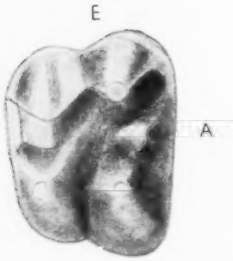

Fig. 3. *Pachynolophus Prevostii* Gerv. Eocène moyen d'Argenton (Indre). Coll. Museum Paris. Don du Musée d'Orléans 1897—6. Dent jugale supérieure droite. 2 fois grandeur naturelle environ.

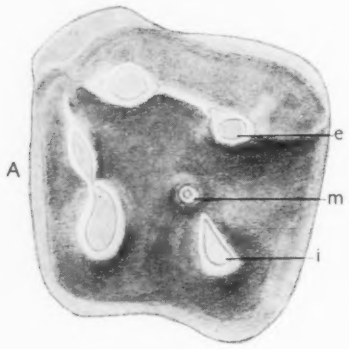

Fig. 4. *Eohippus tapirinus,* Cope. Eocène inférieur (Wasatch), Elk Creek, Wyoming, U.S.A. Coll. British Mus. N. H. Molaire supérieure (M^1) gauche peu abrasée. 5 fois grandeur naturelle environ.

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C. PACHYNOLOPHUS

La genre *Pachynolophus,* de petite taille, a été rencontré dans l'*Eocène inférieur, moyen et supéreur* de France et dans le Bohnherz (Eocène supérieur) de Suisse.

Aux molaires supérieures, les deux tubercules externes, pyramidaux, forment une crête longitudiale; les deux tubercules internes sont coniques et subégaux, les deux tubercules intermédiaires, nets en général. Dans certaines espèces, P^4 est semblable aux molaires, mais à P^3, le tubercule intermédiaire postérieur a dispau (Fig. 3).

Aux molaires inférieures, le type fondamental à deux rangées longitudinales de deux tubercules se maintient, mais les tubercules externes affectent nettement une forme en V aigu, à sommet jugal, alors que les tubercules internes sont coniques.

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D. EOHIPPUS

L'*Eohippus* vécut à l'*Eocène inférieur* (Wasatch beds), en Amérique du nord: Wyoming et Nouveau-Mexique. Il fut donc le contemporain de l'*Hyracotherium,* du *Propachynolophus* et du *Pachynolophus.* Il est surtout intéressant de comparer ses molaires à celles de l'*Hyracotherium.* Chez l'*Eohippus tapirinus* Cope, que j'ai étudié au British Museum Natural History, les molaires supérieures jeunes (Fig. 4) possèdent la même disposition des cuspides que chez l'*Hyracotherium,* mais elles sont réunies par des crêtes, beaucoup plus élevées que chez l'*Hyracotherium vulpiceps* Owen, où elles sont à peine marquées:

1) *crête externe,* unissant les deux tubercules externes;

2) *crête transversale antérieure,* légèrement oblique d'arrière en avant et de dedans en dehors, unissant le tubercule interne antérieur au tubercule intermédiaire antérieur. Cette crête se prolonge un peu au delà du tubercule intermédiaire antérieur, sans atteindre, cependant, le tubercule externe correspondant;

3) *crête transversale postérieure,* de même direction que l'antérieure, mais beaucoup moins nette, n'étant qu'un allongement du tubercule interne postérieur dans la direction de l'intermédiaire postérieur.

La molaire supérieure de l'*Eohippus* est donc plus évoluée que celle de l'*Hyracotherium,* dans le sens de la morphologie dentaire générale des Périssodactyles éocènes, puisque légèrement à crêtes transverses, tout en possédant la crête longitudinale externe si développée chez les *Rhinoceridae,* par exemple.

La molaire inférieure est aussi de type primitif, à quatre tubercules, mais les externes affectent une forme en V à sommet jugal. M_3 avec un talonide.

Considérations générales

Les molaires de l'*Hyracotherium,* comme nous l'avons dit, sont de type fondamental et parabunodonte (de *βουνὸς,* colline), c'est-à-dire que, sur la face

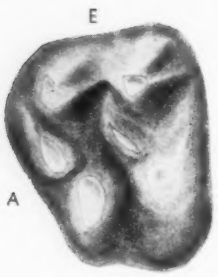

Fig. 5. *Lophiotherium cervulum* Gerv. Eocène supérieur de Saint-Hippolyte-de-Caton (Gard). Coll. Museum Paris. Depéret 1898—21. Molaire supérieure (M^1) gauche. 4 fois grandeur naturelle environ.

triturante, les vallées longitudinales et transversales sont sensiblement de même profondeur. Le type bunodonte ou, plus exactement, parabunodonte, correspond à des nouvements de la mandibule à peu près également développés dans le plan horizontal. Les Mammifères parabunodontes sont des omnivores.

Ce type dentaire évolue, au cours de l'Eocène: il devient toechodonte (de τοιχος, muraille), quoique faiblement, chez le *Propachynolophus,* le *Pachymolophus* et l'*Eohippus,* dont les crêtes transverses se dessinent aux *molaires supérieures,* entre les tubercules internes et les intermédiaires correspondants, tandis qu'aux *molaires inférieures,* les tubercules externes tendent à prendre l'aspect d'un V très fermé.

Cette disposition indique que les mouvements de la mandibule, dans le plan horizontal, sont devenus prédominants dans le sens antéro-postérieur: il s'agit de Mammifères déjà herbivores, mais non exclusivement.

Le type toechodonte se poursuit et s'affirme dans un phylum d'*Equidae* que nous étudierons plus loin.

II. La lignée du Lophiotherium

LOPHIOTHERIUM

Le *Lophiotherium,* de l'*Eocène supérieur* de France et de Suisse, possède des molaires de type encore fondamental; mais, aux dents supérieures, les tubercules intermédiaires, beaucoup plus développés que dans les genres précédents, sont presque aussi volumineux que les externes et les internes. Une crête longitudinale est formée par les deux tubercules externes et, sur la dent peu abrasée du *Lophiotherium cervulum* Gervais (Fig. 5), il existe l'ébauche de deux crêtes transverses, légèrement obliques d'arrière en avant et de dedans en dehors, au delà de chaque tubercule intermédiaire seulement. Cette molaire, moins évoluée que celle de l'*Eohippus,* en diffère aussi et surtout par le grand développement des tubercules intermédiaires.

Les molaires inférieures 1 et 2 sont à deux rangées longitudinales de

deux tubercules, dont les externes, en forme de V à sommet jugal; M_3 avec un talonide.

Les prémolaires ont tendance à se molariser.

Avec Ch. Depéret, j'estime que le *Lophiotherium* représente le type terminal d'un rameau éteint.

III. La lignée du Palaeotherium

PALAEOTHERIUM

Le *Palaeotherium* est le Mammifère le plus caractéristique de l'*Eocène supérieur* de France, d'Angleterre, d'Allemagne méridionale et de Suisse. La plus petite espèce, *Palaeotherium curtum* Cuv., atteignait la taille d'un Porc, la plus grande, *Palaeotherium magnum* Cuv., celle d'un Rhinocéros.

Ce genre, relativement brachyodonte, présente des prémolaires postérieures molarisées dans les formes les plus récentes.

Les molaires supérieures, toujours étroites de dedans en dehors, varient quelque peu avec les espèces. — Chez le *Palaeotherium magnum* Cuv., elles sont encore de type archaïque (Fig. 6): à deux tubercules externes prismatiques, unis dans le sens antéro-postérieur; deux tubercules internes coniques et deux tubercules intermédiaires petits et prismatiques, très nets, indépendants des internes. — Par contre, chez d'autres *Palaeotheriums,* notamment le *Palaeotherium* sp. de l'Ecole des Mines de Paris, du Plateau d'Avron (Fig. 7 en haut): les tubercules externes sont en croissant peu accusé ouvert du côté jugal; les deux tubercules internes, encore coniques, sont unis en une crête légèrement concave vers l'arrière, très oblique d'arrière en avant et de dedans en dehors, aux tubercules intermédiaires correspondants, dont l'antérieur, très petit et prismatique, est discernable, alors que le postérieur se confond avec la crête oblique.

Aux molaires inférieures 1 et 2 (la molaire 3 possédant un talonide), des quatre tubercules fondamentaux, les internes tendent à s'effacer; les externes, en croissant fermé à convexité jugale, aboutissent: l'antérieur, au tubercule interne antérieur, par sa corne postérieure; le postérieur, aux deux tubercules internes (antérieur et postérieur), par l'une et l'autre de ses extrémités.

Une forme assez voisine du *Palaeotherium,* quoique plus évoluée par l'ostéologie de ses membres, sa formule dentaire et la présence d'un large diatème aux maxillaires, est le *Paloplotherium,* qui vécut en Europe, de l'*Eocène moyen* à l'*Oligocène*: ses molaires supérieures, plus longues que larges, présentent des tubercules intermédiaires qui, parfois, ne s'unissent pas au internes, mais sont allongés très obliquement, d'arrière en avant et de dedans en dehors. Parfois aussi, chez le *Paloplotherium minus* Cuv., le tubercule intermédiaire postérieur, qui tend à disparaître, s'unit à l'interne correspondant (Fig. 8 à gauche) pour former une crête si oblique qu'elle en est presque longitudinale.

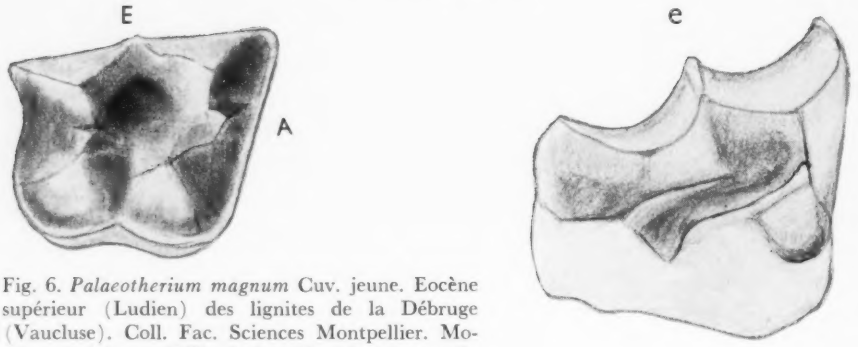

Fig. 6. *Palaeotherium magnum* Cuv. jeune. Eocène supérieur (Ludien) des lignites de la Débruge (Vaucluse). Coll. Fac. Sciences Montpellier. Molaire supérieure (M^1) droite. Grandeur naturelle environ.

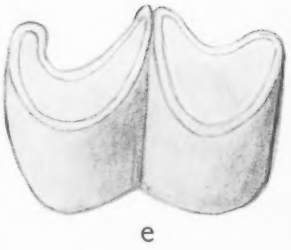

Fig. 7. *Palaeotherium* sp. Eocène supérieur du Plateau d'Avron (S. et O.). Coll. Ecole des Mines Paris. Don de M. Laville, 1893. Molaires droites. En haut, M^3 non abrasée; en bas, M_2 abrasée. 1 fois et demie grandeur naturelle environ.

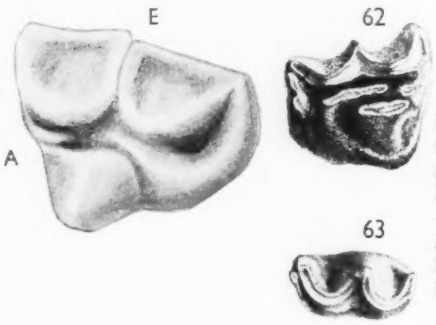

Fig. 8. *Paloplotherium. A gauche: Paloplotherium minus* Cuv. Eocène supérieur du gypse de Montmartre. Coll. Museum Paris. Molaire supérieure (M^3) gauche, non abrasée. — 2 fois grandeur naturelle environ. A droite: *Paloplotherium* sp., de grande taille. *62:* Molaire supérieure droite abrasée. — *63:* Molaire inférieure gauche abrasée. — Grandeur naturelle. — Extrait de W. Kovalevsky.

Les molaires inférieures 1 et 2 sont encore à deux rangées de tubercules: les deux internes, petits et coniques, sont rejoints par les externes, en croissant fermé.

Considérations générales

Les molaires du *Palaeotherium,* par rapport à celles des *Hyracotheriinae* primitifs, tendent vers une bélodontie (de *βέλος*, flèche) relative: aux molaires supérieures, les crêtes transverses, ou presque, chez l'*Eohippus,* deviennent si obli-

ques, dans les espèces évoluées, qu'elles en sont presque antéro-postérieures. — De même, aux molaires inférieures, les crêtes en V très fermé s'ouvrent, ici, en croissant.

Le type bélodonte s'observe aussi chez le *Paloplotherium,* dont les tubercules intermédiaires et internes des molaires supérieures s'allongent si obliquement qu'ils en sont presque antéro-postérieurs. Un fait remarquable est l'étroitesse de ces molaires, qui tendent à ne pas dépasser en largeur les inférieures, rappelant, ainsi, les dents jugales des Proboscidiens et des Rongeurs (toechondontes), alors que les molaires supérieures des *Equidae* demeurent, en général, plus larges que les inférieures.

Au cours de l'évolution, aux molaires supérieures de ces deux genres, les tubercules intermédiaires tendent à disparaître, en commençant par le postérieur, alors qu'aux molaires inférieures, les tubercules internes, qui subsistent, diminuent, l'un et l'autre, d'importance.

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IV. La lignée de l'Anchilophus et de l'Anchitherium

Les *Equidae* de ce rameau, relativement brachyodontes, possèdent une formule dentaire complète et des prémolaires postérieures, molariformes; M_3 avec un talonide. Ils sont connus de l'Eocène moyen au Miocène supérieur, en Europe et en Amérique du nord, au Miocène et au Pliocène, en Asie.

A. ANCHILOPHUS

Chez l'*Anchilophus,* de l'*Eocène moyen et supérieur* d'Europe, les molaires supérieures, aussi larges que longues, sont de type archaïque, avec l'ébauche d'une crête longitudinale externe et de deux crêtes transverses obliques d'arrière en avant et de dedans en dehors, entre chaque tubercule interne et le tubercule intermédiaire correspondant; ces crêtes atteignent les tubercules externes.

Aux molaires inférieures, des deux tubercules internes, l'antérieur s'est divisé en deux (dans le sens antéro-postérieur), alors que le postérieur est demeuré conique. Des deux tubercules externes, en V assez ouvert, l'antérieur aboutit au tubercule interne tout antérieur, par sa branche postérieure, le postérieur, au tubercule médian (division du tubercule interne antérieur) et au tubercule interne postérieur, par ses deux extrémités.

B. MESOHIPPUS

Le *Mesohippus* vécut à l'*Oligocène* (White River beds) en Amérique du nord.

Le *Mesohippus Bairdi* Leidy, que j'ai étudié à l'Université d'Upsal, était de la taille d'un Mouton. Ses molaires supérieures (Fig. 9) présentent deux tubercules externes un peu crescentiformes, unis en une crête longitudinale, et deux crêtes transverses, obliques d'arrière en avant et de dedans en dehors, plus

Fig. 9. *Mesohippus Bairdi* Leidy. Oligocène (Oreodon Beds) de White River. Coll. Fac. Upsal. Les trois molaires supérieures gauches, peu abrasées. 2 fois grandeur naturelle environ.

accusées que chez l'*Eohippus* et l'*Anchilophus;* elles atteignent, ou presque, la crête externe, après avoir uni chaque tubercule interne à l'intermédiaire correspondant.

Les molaires inférieures sont à deux tubercules externes en V largement ouvert, à sommet jugal, qui rejoignent, de la même manière que chez l'*Anchilophus,* les tubercules internes (dont l'antérieur est presque bicuspide, le postérieur, simple et conique).

C. ANCHITHERIUM

L'*Anchitherium* est connu en Europe (France, Allemagne méridionale, Autriche) par une seule espèce: *Anchitherium aurelianense* Cuv., du *Miocène supérieur,* rencontrée aussi en Asie. Aux molaires supérieures, les tubercules externes, prismatiques et légèrement en croissant, forment encore une crête longitudinale; les tubercules internes, forts et coniques, sont unis par des crêtes obliques d'arrière en avant et de dedans en dehors aux tubercules intermédiaires correspondants, très petits, étroits et en croissant; ces crêtes atteignent les tubercules externes (Fig. 10, 52 et 53).

Les molaires inférieures ressemblent à celles de l'*Anchilophus* et du *Mesohippus* (Fig. 10, 64).

L'*Anchitherium* s'éloigne surtout du *Mesohippus* par le faible développement, aux molaires supérieures, des tubercules intermédiaires, qui subsistent cependant.

Considérations générales

Dans ce rameau d'*Equidae,* le type molaire est proche encore de celui des *Hyracotheriinae* primitifs; mais, au maxillaire supérieur, les crêtes transverses sont plus accusées, tout en demeurant peu obliques, et les tubercules intermédiaires tendent à diminuer d'importance. — Les molaires inférieures, à crêtes externes en V ouvert et à trois tubercules internes coniques font, en quelque sorte, la transition entre celles des *Hyracotheriinae* archaïques (quatre tubercules, crêtes transverses ou en V très fermé) et celles des *Equinae* (cinq tubercules dont les externes, en croissant aplati).

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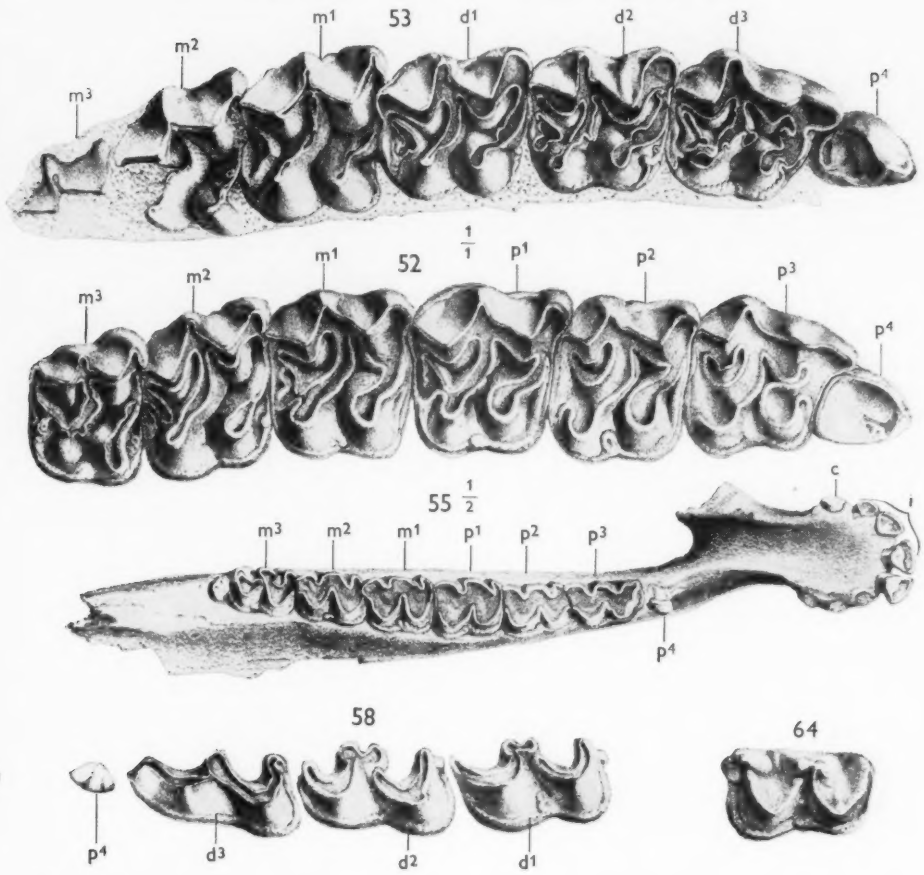


Fig. 10. *Anchitherium aurelianense* Cuv. *52.* Série complète des dents jugales supérieures, du côté droit, d'un adulte. Grandeur naturelle. *53.* Série des dents jugales supérieures, du côte droit, d'un jeune animal, avec les trois molaires temporaires et la 1ère prémolaire, qui n'a pas de prédécesseur. Grandeur naturelle. *55.* Mâchoire inférieure, fracturée, d'un adulte. 1/2 de la grandeur naturelle. *58.* Dents jugales inférieures gauches d'un jeune animal: 1ère prémolaire et les trois molaires temporaires. Grandeur naturelle. *64.* Molaire inférieure droite non abrasée d'un adulte. Grandeur naturelle Extrait de W. Kovalevsky. Noter que les molaires temporaires et les prémolaires sont, ici, numérotées d'arrière en avant, contrairement à la règle générale.

Il s'agit d'un phylum toechodonte éteint, plus proche, par ses molaires, des *Rhinoceridae* primitifs que des *Equinae,* qui s'est développé simultanément dans l'Ancien et le Nouveau Mondes, de l'Eocène à la fin du Miocène (et même au Pliocène, en Chine). L'*Anchitherium* en est le représentant terminal, dans l'Ancien Monde.

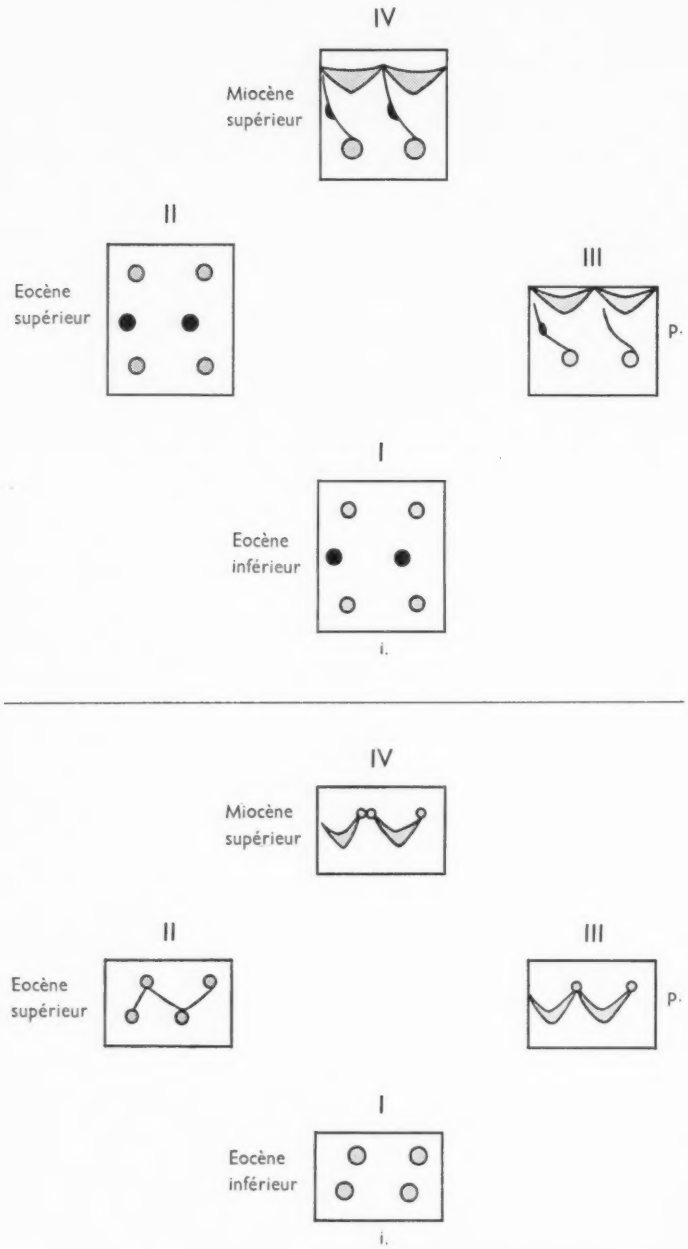


Fig. 11. Schéma de l'évolution de la molaire supérieure (en haut) et inférieure (en bas) des *Equidae:* de *l'Hyracotherium* (I) au *Lophiotherium* (II), au *Palaeotherium* (III) et à *l'Anchitherium* (IV). — i. côte interne. — p. côte postérieur. — En noir: tubercules intermédiaires, aux molaires supérieures.

La toechodontie révèle l'adaptation de ces *Equidae* à un régime herbivore, moins exclusif, pourtant, que la bélodontie des formes encore actuelles.

V. La lignée de l'Equus : Equinae

Les *Equinae* sont plus ou moins hypsélodontes, avec des prémolaires molariformes, sauf Pl très petite, caduque, souvent absente. Au niveau des dents jugales, le cément est, en général, abondant.

A l'état fossile, ils sont connus dans le Miocène moyen d'Amérique du nord; dans le Miocène supérieur, le Pliocène et le Pléistocène d'Amérique du nord, d'Asie, d'Europe et d'Afrique; dans le Pléistocène d'Amérique du sud.

Actuellement, répandus dans le Monde entier par la domestication, ils ne sont indigènes qu'en Asie et en Afrique.

A. MERYCHIPPUS

De nombreuses formes proches du *Merychippus* ont été décrites, dont il est difficile de tenir compte dans cette étude.

Le *Merychippus,* le plus ancien, semble-t-il, et le moins spécialisé des *Equinae,* vécut, en Amérique du nord, du *Miocène moyen au Pliocène inférieur.*

Aux molaires supérieures, non seulement les tubercules externes, mais aussi les intermédiaires, volumineux, sont en forme de croissant ouvert du côté jugal et unis deux à deux dans le sens longitudinal. Les deux tubercules internes, réduits au contraire, sont reliés aux tubercules intermédiaires par de courtes crêtes presque transverses, obliques d'arrière en avant et de dedans en dehors (Fig. 12, en haut).

Aux molaires inférieures, le dédoublement du tubercule antéro-interne dans le sens longitudinal est net, comme dans la lignée de l'*Anchilophus*: il se maintiendra jusqu'au genre *Equus.* Des deux tubercules externes, en croissant à concavité linguale, l'antérieur aboutit à un seul tubercule interne, tout antérieur, par sa corne postérieure; le postérieur, au tubercule interne médian (division de l'interne antérieur) et au tubercule interne postérieur, par l'une et l'autre de ses extrémités.

Les molaires inférieures ne diffèrent, en somme, de celles des genres proches de l'*Anchitherium* que par la forme de ses tubercules externes, en croissant, au lieu d'être en V. — Notons aussi une expansion postéro-interne du tubercule externe postérieur, tendant à former un quatrième tubercule interne, disposition qui persiste et s'accuse, au cours de l'évolution des *Equinae.*

B. HIPPARION

L'*Hipparion,* qui vécut au *Miocène supérieur* et au *Pliocène* en Asie, en Europe, en Afrique et en Amérique du nord, était, quant à la taille, intermédiaire entre l'Ane et le Zèbre. Sa formule dentaire était:

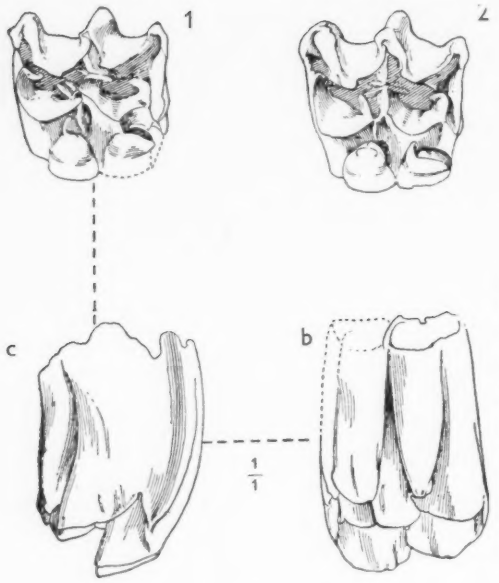


Fig. 12. *Merychippus* des Coll. de l'Amer. Museum. Prémolaire supérieure molariforme (P^4), du côté gauche, intra-alvéolaire, cuspidée et sans cément. *1. Merychippus paniensis* Cope. Miocène moyen de Pawnee Creek, Colorado. 1. face triturante. — c. face antérieure. — b. face latérate interne. *2. Merychippus calamarius* Cope. Pliocène inférieur de Snake Creek, Sioux County, Nebraska; face triturante. Grandeur naturelle. Extrait de H. F. Osborn.

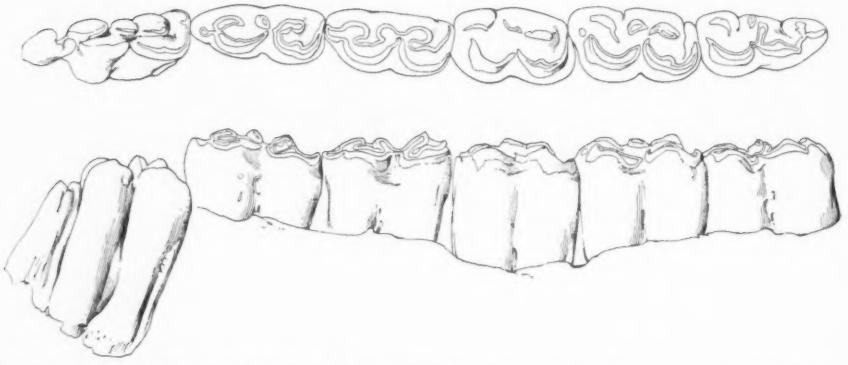
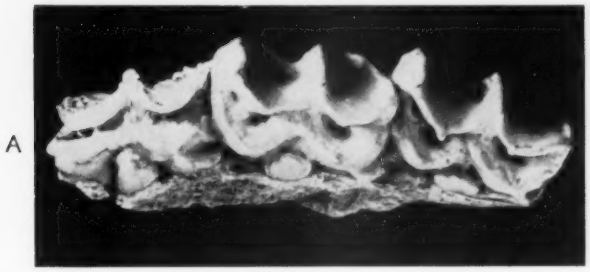


Fig. 13. *Merychippus eohipparion* Osborn. Miocène moyen des Pawnee Creek beds, Colorado. Coll. Amer. Museum. Série des dents jugales inférieures droites. L'avant est à droite. En haut: faces triturantes. En bas: faces latérales externes. — La dernière molaire (M_3), avec un talonide, est intra-alvéolaire, cuspidée et sans cément. 3/4 de la grandeur naturelle. Extrait de H. F. Osborn.

$I\frac{3}{3}, C\frac{1}{1}, P\frac{4-3}{3}, M\frac{3}{3}$, avec des dents jugales à croissance moins prolongée que celles du Cheval (*Equus*) et une 1ère prémolaire supérieure (P^1), caduque de bonne heure.

Les molaires supérieures (Fig. 14, en haut et au milieu), plus allongées dans le sens antéro-postérieur que celles du *Merychippus,* comportent les six tubercules fondamentaux, dont les deux externes et les deux intermédiaires (légère-



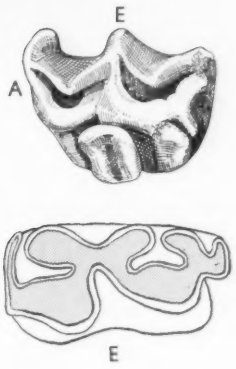


Fig. 14. *Hipparion* sp. du Pontien de Chine, Province Shansi, Pao te Hsien. *En haut:* les trois prémolaires molariformes supérieures (P^2, P^3, P^4) non abrasées, du côté gauche. *Au milieu:* molaire supérieure gauche, non abrasée. *En bas:* schéma d'une molaire inférieure gauche, abrasée. Coll. Fac. Upsal. — Grandeur naturelle environ.

ment décalés vers l'avant, par rapport aux externes et aux internes, comme au début de l'évolution), plus volumineux encore et plus allongés que chez le *Merychippus,* affectent une forme en croissant de lune ouvert du côté jugal, très caractéristique. Les internes, de faible taille, sont: l'antérieur, indépendant sur une grande hauteur, qui forme une sorte d'îlot au niveau de la surface d'abrasion; le postérieur, plus petit encore, en partie accolé à la région médiane de l'intermédiaire correspondant.

Les molaires inférieures (Fig. 14, en bas), assez comparables à celles du *Merychippus,* mais plus allongées, présentent aussi des tubercules externes en croissant plus ouvert et plus aplati.

C. EQUUS

Le genre *Equus,* qui vécut au *Pliocène* en Asie (couches des Siwalik, dans l'Inde), caractérise, en Europe, le *Pléistocène,* dont il marque le début. Il est également connu en Asie, en Afrique, en Amérique du nord et du sud, au Pléistocène. Actuellement, domestiqué dans le Monde entier, il n'est indigène qu'en Asie et en Afrique.

Sa formule dentaire est complète. La *1ère dent jugale* (Pl), très réduite de volume, n'est précédée ni suivie d'aucune autre: c'est la «dent de loup» des vétérinaires; elle tombe d'assez bonne heure. Chez le Cheval actuel (*Equus caballus* L.), j'ai constaté qu'elle commence à se calcifier très longtemps après les molaires

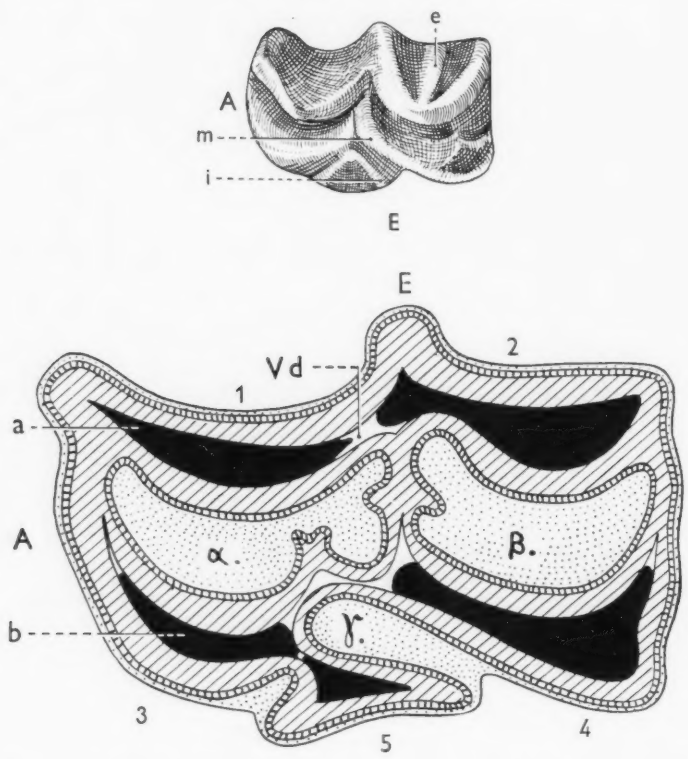


Fig. 15. *Equus caballus* L. (Cheval) actuel. *En haut:* molaire temporaire supérieure gauche, cuspidée, d'un Cheval pur-sang anglais, nouveau-né. Coll. Museum Paris. — e. rangée cuspidienne externe. — m. rangée cuspidienne intermédiaire ou moyenne. — i. rangée cuspidienne interne, formée d'une seule cuspide, l'antérieure (la postérieure, encore visible, n'est plus qu'une dépendance de la cuspide intermédiaire postérieure, à laquelle elle est soudée). — Grandeur naturelle environ. *En bas:* 3ème molaire temporaire supérieure (Mt^4) gauche d'un jeune Cheval. Coll. Museum Paris. Coupe à 15 mm des cuspides les plus élevées, les externes. Il existe une chambre pulpaire (en noir) par cuspide originelle. — a. chambres pulpaires correspondant aux 2 cuspides externes. — b. chambres pulpaires correspondant aux 2 cuspides intermédiaires et à la cuspide interne unique, l'antérieure. — Vd. vaso-dentine. — Du cément, en pointillé, remplit les tubes intermédiaires, α, β, et le sinus interne, γ. — L'ivoire est en hachures, l'émail, en hachures fines, la vaso-dentine, en blanc. — Grandeur réelle: 40 mm.

temporaires, c'est pourquoi j'estime, avec Ch. S. Tomes, qu'il s'agit, non d'une 1ère molaire temporaire, mais d'une prémolaire, le Cheval n'ayant, alors, que trois molaires de lait.

Les *canines,* rudimentaires chez la femelle, sont bien développées chez le mâle. — Il existe une «barre» plus accusée que chez les autres *Equinae,* entre la canine et les prémolaires.

Les molaires supérieures non abrasées (chez le nouveau-né, par exemple,

Fig. 16. *Equus caballus* L. (Cheval) jeune, des gisements pléistocènes d'Œtrange (Grand-Duché de Luxembourg). Fragment de mâchoire supérieure, avec les molaires temporaires (Mt^2, Mt^3, Mt^4) en place, de chaque côte, et l'alvéole de la «dent de Loup» (P^4) particulièrement développée. 3/4 de la grandeur naturelle. Extrait de V. Ferrant et M. Friant.

où il s'agit de molaires temporaires: Fig. 15, en haut) ressemblent à celles de l'*Hipparion,* avec des tubercules externes et des tubercules intermédiaires, tous quatre volumineux et en croissant, unis deux à deux dans le sens longitudinal; mais les deux tubercules internes sont plus réduits encore: l'antérieur s'unit, par une courte crête oblique d'arrière en avant et de dedans en dehors, au tubercule intermédiaire antérieur, alors que l'interne postérieur s'accole à l'intermédiaire correspondant, pour en constituer une dépendance.

Les molaires inférieures non abrasées (Fig. 18, en haut) comportent deux tubercules externes qui ne sont plus en croissant, mais ont pris quelque peu l'aspect d'une portion de rectangle à angles émoussés; alors que les tubercules

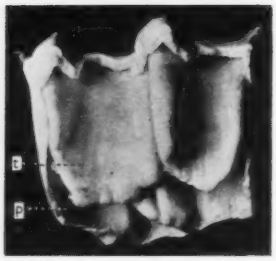
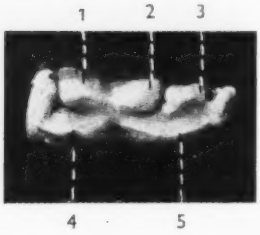


Fig. 17. *Equus caballus* L. (Cheval) jeune, actuel. 2ème molaire temporaire supérieure droite (Mt^2), après ablation de la paroi externe; vue vestibulaire un peu inférieure, pour montrer les tubes intermédiaires déjá fermés, les trois racines de la molaire temporaire n'existent pas encore. Coll. Museum Paris. — t. tube intermédiaire. — p. chambre pulpaire. La face antérieure est à droite. Grandeur naturelle environ.



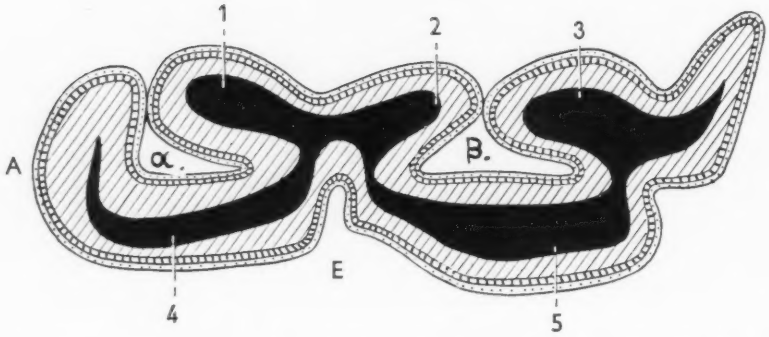


Fig. 18. *Equus caballus* L. (Cheval) actuel. *En haut:* 2ème molaire temporaire inférieure (Mt_3) gauche, cuspidée, d'un jeune Cheval. Coll. Museum Paris. 1, 2, 3, tubercules internes (1 et 2 représentant l'antéro-interne dédoublé). — 4, 5, tubercules externes. — Grandeur naturelle environ. *En bas:* 3ème molaire temporaire inférieure (Mt_4) gauche d'un jeune Cheval. Coll. Museum Paris. Coupe à 10 mm des cuspides les plus élevées, les externes. — α, β, sinus. — Les autres indications comme figure 15, en bas. — Grandeur réelle: 43 mm.

internes sont encore au nombre de trois: l'antérieur divisé en deux dans le sens longitudinal, comme chez tous les *Equinae,* et le postérieur, simple et conique. De même que dans la lignée de l'*Anchitherium* et chez les autres *Equinae,* des deux tubercules externes, l'antérieur s'unit, par sa corne postérieure, au tubercule interne le plus antérieur; le postérieur, au tubercule médian (division du tubercule interne antérieur) et au tubercule interne postérieur, par ses deux extrémités.

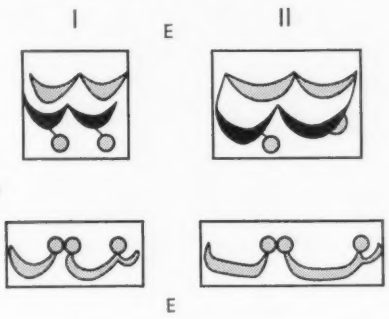


Fig. 19. Schéma des molaires: supérieure, en haut; inférieure, en bas, du *Merychippus* (I) et de *l'Equus* (II). En noir: tubercules intermédiaires, aux molaires supérieures.

On constate donc que l'évolution des molaires, au cours de la phylogénie, permet, seule, d'interpréter ces dents, si complexes chez l'*Equus*.

La série des *coupes transverses d'une molaire supérieure* d'*Equus caballus* L. met en évidence que les cuspides, en s'unissant les unes aux autres, forment deux «tubes intermédiaires» : α, en avant, β, en arrière, qui, chez l'adulte, sont remplis de cément (Fig. 15, en bas, et Fig. 17). Il existe, en outre, un sinus interne, γ, qui devient, lui aussi, un tube intermédiaire, mais très tard au cours du développement. Ces tubes se ferment inférieurement, tandis que les parois de la dent poursuivent leur croissance (Fig. 17).

Les coupes transverses d'une *molaire inférieure* d'*Equus caballus* L. (Fig. 18, en bas) montrent que les cuspides, par leur union, forment deux sinus internes, profonds : α, en avant, β, en arrière; ces sinus se ferment très tard, pour constituer des tubes de quelques millimètres de longueur seulement.

Une disposition très comparable des deux tubes principaux, aux molaires supérieures, et des deux sinus, aux molaires inférieures, existe chez tous les *Equinae*, d'après le dessin de la table d'usure de leurs dents jugales.

Considérations générales

Les *Equinae* sont caractérisés par:

1°. L'allongement antéro-postérieur, progressif, des dents molariformes.

2°. Aux molaires supérieures, le grand développement des tubercules intermédiaires, qui tendent à égaler les externes, tous quatre affectant la forme d'un croissant très ouvert du côté jugal et unis deux à deux dans le sens longitudinal; l'affaiblissement des tubercules internes, dont le postérieur est à peine discernable chez l'*Equus*.

3°. Aux molaires inférieures, une morphologie qui accuse celle des molaires inférieures de la lignée de l'*Anchitherium*; mais les tubercules externes, au lieu d'être en V, deviennent en croissant ouvert lingualement, puis le croissant s'étale et s'aplatit, tandis que les trois tubercules internes, coniques, subsistent.

Les *Equinae* sont des «bélodontes typiques», par leurs molaires à tubercu-

les principaux en croissant, de plus en plus ouvert, formant des crêtes longitudinales, disposition en rapport avec un régime herbivore très net.

Conclusions

I. Au début de leur évolution, à l'Eocène inférieur, les *Equidae,* comme tous les Mammifères euthériens archaïques, présentaient des molaires de type fondamental, à formule cuspidienne : $\frac{\text{III (2)}}{\text{II (2)}}$ à morphologie parabunodonte; tel était l'*Hyracotherium.* Ce type se maintient, durant l'Eocène, avec l'indication d'une faible toechodontie, chez le *Propachynolophus,* le *Pachynolophus* et l'*Eohippus.*

II. Les *tubercules intermédiaires des molaires supérieures,* plus petits que les autres dans le type fondamental, *augmentent de volume* et sont aussi développés que les externes et les internes chez le *Lophiotherium,* de l'Eocène supérieur.

III. Les faibles crêtes transverses constituées entre les tubercules internes et les intermédiaires correspondants, aux molaires supérieures de l'*Eohippus,* deviennent si obliques qu'elles en sont presque longitudinales, tandis que le tubercule intermédiaire postérieur s'efface. Aux molaires inférieures, les tubercules externes se développent en croissant. Il s'établit, ainsi, un type que *tend vers la bélodontie*: c'est celui du *Palaeotherium,* de l'Eocène supérieur.

IV. Dans la lignée de l'*Anchitherium* (de l'Eocène au Pliocène), le *type toechodonte* est réalisé par la constitution, aux molaires supérieures, de crêtes presque transverses, où les tubercules intermédiaires subsistent, quoique très faibles. Aux molaires inférieures, les deux tubercules externes sont en V à sommet jugal, alors que des deux internes, l'antérieur s'est dédoublé dans le sens longitudinal.

V. Les *Equinae,* du Miocène à l'Actuel, très spécialisés, sont caractérisés par des molaires supérieures à deux tubercules externes et deux tubercules intermédiaires en forme de croissant volumineux, ouvert du côté jugal, alors que les tubercules internes ont diminué d'importance (le postérieur surtout), au cours de l'évolution. Aux molaires inférieures, les deux tubercules externes, en croissant de plus en plus aplati, rejoignent les trois tubercules internes, déjà constitués dans la lignée de l'*Anchitherium.* Les *Equinae* sont nettement bélodontes. On peut difficilement les rattacher à un groupe plus ancien, si ce n'est celui de l'*Hyracotherium.*

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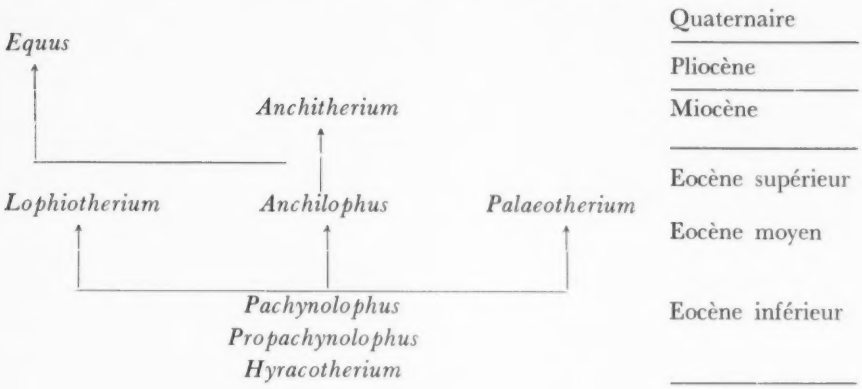
La morphologie des molaires chez les Equidae

Schema de l'evolution des Equidae



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Comme l'a dit magistralement M. A. C. HINTON, pour les Rongeurs, en 1926, «si les vues ci-dessus exprimées sont entendues, alors les brillantes généralisations qui constituent la fameuse «Théorie trituberculaire», à l'origine de tant de recherches productives en Paléontologie, ne s'applique pas» aux *Equidae*.

Il est impressionnant de constater que l'évolution dentaire des *Equidae* correspond à une adaptation progressive, non moins accusée, du squelette des extrémités à la course, dont voici un schéma, de l'*Hyracotherium* à l'*Equus*.

Hyracotherium ——————————→ Equus

Patte antérieure	Radius + Cubitus	Régression du Cubitus
	4 Doigts : 2—3—4—5	1 Doigt (3) et 2 Stylets
Patte postérieure	Tibia + Péroné	Régression du Péroné
	3 Doigts : 2—3—4	1 Doigt (3) et 2 Stylets

Toutefois, les nombreux stades évolutifs du squelette des *Equidae*, depuis l'Eocène jusqu'au Quaternaire, ne peuvent donner aucune idée des phyla si divers, marqués par la morphologie des molaires, en rapport avec l'alimentation, qui a varié avec les groupes et au cours des Temps.

Chez ces Périssodactyles, l'évolution s'est poursuivie, à la fois, dans l'Ancien et le Nouveau Mondes, en séries parallèles, très rarement identiques; ce qui permet de penser que les deux Mondes ont communiqué, à certaines périodes, au moins, dès le début des Temps tertiaires.

Résumé

La morphologie si complexe des molaires du Cheval (*Equus*), le plus spécialisé des *Equidae*, à tous points de vue, ne peut être interprétée que par l'étude de ces dents au stade non abrasé (le seul anatomique) et par comparaison avec les molaires d'*Equidae* plus archaïques.

A partir de l'*Hyracotherium*, de l'Eocène inférieur d'Europe, qui possède le type molaire fondamental : $\frac{\text{III (2)}}{\text{II (2)}}$, on voit se détacher de nombreux phyla, au cours du Tertiaire. Mais, dans l'état actuel de nos connaissances, le rameau devant aboutir à l'*Equus*, le plus herbivore de tous, ne se distingue qu'à partir du Miocène, en Amérique du Nord.

Summary

The so complex molar morphology of the Horse (*Equus*), the most specialised of the *Equidae*, at any point of view, may only be explained by the study of the molars when not yet worn (the anatomical stage) and with comparison to most archaic *Equidae*'s ones.

From *Hyracotherium* (Lower Eocene Period), that possesses the "fondamental" molar type, $\frac{\text{III (2)}}{\text{II (2)}}$, many phyla stand out, during the Tertiary Era. But, in the actual state of our knowledge, the branch leading to *Equus*, the most herbivorous of all, is described from the Miocene Period only and in North America.

Références

Les travaux sur les *Equidae* fossiles et actules sont fort nombreux. Nous ne citerons que les principaux ouvrages consultés.

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